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BREEDING AND IMPROVEMENT OF FARM ANIMALS

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Breeding and Improvement
of
Farm Animals

BY

VICTOR ARTHUR RICE
Professor of Animal Husbandry
The Massachusetts State College

WITH CHAPTERS ON

The Endocrine Basis of Reproduction and Artificial Insemination

BY

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Purdue University

THIRD EDITION
FOURTH IMPRESSION

McGRAW-HILL BOOK COMPANY, INC.
NEW YORK AND LONDON
1942

BREEDING AND IMPROVEMENT OF FARM ANIMALS

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THE MAPLE PRESS COMPANY, YORK, PA.

To

the Memory of

DR. DANIEL HARVEY HILL
President of the North Carolina State College, 1908–1916

and

DR. ROSCOE WILFRED THATCHER
President of the Massachusetts State College, 1927–1932

in lower organisms are difficult or impossible of exemplification in the higher species, it is a virtual certainty that they are at work. Therefore a full understanding of the basic principles is necessary if the breeder is to handle, in the most intelligent and profitable manner, his practical problems of selection.

Section IV is devoted to what is often called the *art of breeding*, which may be summed up in one word *selection*. This term has both a present and a future connotation, since a breeder is constantly selecting from among the best animals making up his herd or flock on the basis of their pedigrees and performance, and he is also anticipating future selection by planning matings to create new animals of a preconceived pattern. Selection, therefore, involves the various systems of breeding both among related and unrelated individuals. In the final chapter the reader can glance backward over the trail that animal breeders and scientists have blazed and look forward to try to foresee "the shape of things to come."

It is the author's hope that this book will be stimulating and helpful to students of breeding both in classrooms and on livestock farms.

Many friends have assisted the author in the preparation of this book; among them Drs. H. H. Plough and Charles L. Sherman of Amherst College; Dr. Harry L. Shapiro of the American Museum of Natural History, New York; Mr. Bradford Knapp, Jr., of the Bureau of Animal Industry, Washington, D.C.; and Dr. G. Chester Crampton, Dr. John B. Lentz, Dr. Frank H. Hays and Mr. Floyd Johnson of the Massachusetts State College. Special thanks are due Dr. F. N. Andrews, of Purdue University, Dr. Arthur B. Chapman, of the University of Wisconsin, and Dr. Hugh C. McPhee, Dr. Ralph W. Phillips, and Dr. Ralph G. Schott of the Bureau of Animal Industry, Washington, D.C., for their suggestions and constructive criticisms. The author is also greatly indebted to Mr. Talcott Edminster for assistance in reading proof, and to Miss Evelyn Day, who in some ingenious manner deciphered the original manuscript and put it through a typewriter.

The author is indebted to Prof. R. A. Fisher and to Messrs. Oliver & Boyd, of Edinburgh, for permission to reprint Tables 29 and 31 from their book *Statistical Methods for Research Workers*, 8th edition (1941).

Grateful acknowledgment is also made to various authors and publishers for permission to use certain of their materials.

If the reader is curious as to the sources of the ideas herein expressed, he may discover them in great measure through consulting the references listed at the close of each chapter.

VICTOR ARTHUR RICE.

AMHERST, MASS.,
March, 1942.

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An artist, modeling in plastic clay or conjuring with marble, brings forth a conception that the world acclaims a triumph. He deals, however, with his materials direct, and they respond instantly to his slightest touch, as he toils toward a preconceived ideal. There is no resistance to his manipulations.

What, then, should be our estimate of the work of one who has first to conceive the figure in his brain; whose only tools are the laws of heredity, selection, inbreeding, outcrossing, and alimentation; whose only materials are flesh and blood, unapproachable except by indirection; who battles ever against the stubborn forces of atavism or reversion to ancestral forms; who seeks, and succeeds in producing, a creature pulsating with life, exquisitely fashioned, down to the minutest detail, not only a thing of beauty in itself—which artists try, sometimes with ill success, to reproduce on canvas or in bronze—but a creation that serves as well the highest utilitarian purpose?

The breeder of animals (or plants) directs the spark of life itself. The possibilities of his art are almost infinite.—A. H. SANDERS.

THE NATIONAL GEOGRAPHIC MAGAZINE,
December, 1925.

SECTION I

Animals and Man Up to the Present

CHAPTER I

ANIMAL BREEDING—PRESENT AND PAST

Animal breeding is one of the largest industries in the United States. It involves 200 million farm mammals, 700 million poultry and other birds, in addition to an innumerable host of dogs, cats, rats, rabbits, foxes, ferrets, and other fur bearers, not to mention among others guinea pigs, guppies, and goldfish. For some it is a hobby; for others a grim reality, because its proceeds must provide the cash to operate a farm and maintain a home. In terms of food, clothing, and the maintenance or increase of soil fertility, every person in the United States has a stake in its success.

Hobbyist and realist are trying in most instances to shape the external form of their animals according to some preconceived plan and at the same time to include within this desirable exterior form some combination of mental and physiological characters that will have a high commercial or aesthetic value. The horseman wants speed and stamina; power, patience, and persistence; easy gait and companionability. The cattleman wants a compact animal that will fatten rapidly into a carcass of good quality, a "typy" cow that will yield a large amount of milk of a high quality. The sheepman wants quality and quantity in both carcass and wool; the hogman as much high-quality pork as he can get from each sow in his herd each year. The dog fancier wants looks, smartness, companionability, and sometimes utility.

Can these various combinations be had in single animals? The answer obviously is "yes," because we have had such animals in the past and have some of them today. Can we so breed our animals that they not only will have these desirable combinations of qualities but also will be able to pass them on to their offspring? The procedure for accomplishing the latter purpose is now known, and the purpose of this book will be to demonstrate the principles underlying reproduction, hereditary transmission, and variation and to show how selection involving the various systems of breeding can be made to yield certain definite results.

Livestock Trends in the United States.—Table 1 depicts the rise in the number of horses until the motor began to supplant the horse and his consequent decline in numbers. It shows the number of meat animals holding about steady, though it should not be forgotten that our meat animals now mature more rapidly than formerly, the quicker turnover actually meaning more product from a fewer number of animals. It also shows a steady rise in the number of dairy animals. Many factors, of course, influence the numbers of animals kept on farms from year to year. The magnitude of the total value of American livestock and the meagerness of the average value stand in marked contrast to each other. Both of these points indicate opportunity for the livestock breeder.

A compilation by the Bureau of Crop Estimates shows: "Of every $100 worth of products sold by all who reported (10,000), approximately $36 were for live animals, $20 were for the products of livestock, $40 were

TABLE 1.—NUMBER AND AVERAGE VALUE PER HEAD OF THE VARIOUS CLASSES OF FARM LIVESTOCK IN THE UNITED STATES, 1880–1940*

Year	Horses on farms		Mules on farms		Dairy cattle	
	Number†	Average value	Number†	Average value	Number†	Average value
1880	10,903	$ 53.74	1,878	$ 61.74	11,754	$23.31
1890	15,732	69.27	2,322	77.61	15,000	22.30
1900	17,856	43.56	3,139	51.46	16,544	31.30
1910	19,972	107.70	4,239	119.98	19,450	35.40
1920	20,091	96.45	5,651	148.29	21,455	81.51
1930	13,742	69.98	5,382	83.93	23,032	82.70
1940	10,616	77.43	4,321	114.53	25,334	57.22

Year	Cattle other than milk cows		Sheep		Hogs, including pigs	
	Number†	Average value	Number†	Average value	Number†	Average value
1880	31,593	$ 15.75	44,867	$ 2.18	44,327	$ 4.40
1890	45,014	15.16	42,693	2.29	48,130	4.80
1900	43,195	24.67	45,065	2.97	51,055	5.36
1910	39,543	19.20	46,939	4.06	48,072	9.05
1920	48,945	39.99	37,328	10.59	60,159	20.00
1930	37,971	40.38	45,577	9.00	55,705	13.45
1940	43,435	30.86	48,473	6.33	58,312	7.79

* *U.S. Dept. Agr. Yearbook*, Agricultural Marketing Service figures as of Jan. 1, 1880–1940. Figures for 1940 are preliminary.

† 000 omitted.

for crops, and $4 for miscellaneous items." Though not all-inclusive, the report states that "complete returns from all farmers probably would not materially modify these figures."

Value of Average Animal.—The modest value of the average horse, mule, cow, sheep, or pig should provoke serious thought on the part of livestock breeders. During the past 50 years (by 10-year intervals) the average value of the different classes of livestock has been: horse $77.40, mule $99.30, dairy cow $51.74, all cattle $36.26, sheep $5.87, swine $10.08. These average values indicate that billions of dollars worth of materials are being produced annually in the United States with low-grade inefficient animals. Such economic waste should be checked as soon as possible.

The U.S. Department of Agriculture is sponsor for the statement that the present low average yield of milk (4,575 lb.) and of fat (181 lb.) by our dairy cows is largely due to the fact that two-thirds to three-fourths of the dairy bulls in the United States are unregistered animals about whose transmitting abilities little or nothing is known. This department also states that only 4 per cent of our dairy cattle are registered and that only about 2 or 3 per cent of the swine in the United States are purebred and registered with about the same figures applying to beef cattle and sheep. Records kept at the large livestock marketing centers indicate that only about 10 to 15 per cent of the cattle coming to market classify in the choice and prime classes and that only about 30 to 40 per cent of the sheep likewise fall into the highest grades as carcasses. No doubt

TABLE 2.—MILK AND FAT PRODUCTION OF PUREBREDS*

Breed	Number of records	Average days	Average pounds milk	Average pounds fat
Holstein	45,445	351	16,737.4	574.3
Holstein	17,323	299	13,986.0	477.0
Brown Swiss	1,272	365	13,793.4	555.45
Brown Swiss	1,204	305	10,854.0	440.07
Guernsey S.	42,866	365	10,450.9	518.1
Guernsey D.	15,877	365	10,532.8	525.8
Guernsey T.	10,001	305	8,040.8	400.6
Jersey	32,068	365	9,149.0	491.28
Jersey	25,050	305	8,016.0	433.33
Ayrshire	7,129	365	10,469.0	416.49
Ayrshire	2,074	305	10,489.0	422,69
Dutch Belted	100	363.8	10,844.32	414.09
Shorthorn	10,121	365	9,432.0	386.71
Red Polled	1,144	365	8,827.0	381.24
Devon	41	365	7,394.5	314.51

* New England Homestead, Springfield, Mass., Sept. 6, 1941.

this is partially controlled by feed conditions, but the major aspect of the problem is that many of our animals are not bred so that they have a possibility of getting into these classes.

Table 3 shows the trend in total numbers and total value of farm livestock in the United States by decades for the past 60 years and the trend in human population. It shows that the breeding of livestock is one of the most important types of endeavor in this country.

TABLE 3.—TOTAL NUMBERS AND VALUE OF LIVESTOCK AND HUMAN POPULATION, UNITED STATES, 1880–1940

Year	Number all farm livestock*	Value all farm livestock	Human population, United States*
1880	120,990,000	$1,576,636,520	50,156,000
1890	165,286,000	2,418,774,100	62,948,000
1900	170,315,000	2,581,751,910	75,994,000
1910	178,355,000	4,649,803,510	91,972,000
1920	196,875,000	7,383,500,260	105,711,000
1930	185,464,000	5,995,084,680	122,775,000
1940	196,491,000	4,904,307,000	131,669,000

* To even thousands.

Value of Purebred Animals.—The monetary value of purebred animals always exceeds that of grade animals. Cow-test-association figures for 1932 showed that 17,465 randomly selected registered cows averaged 8,400 lb. of milk testing 4.08 per cent, or 343 lb., of butterfat for the year, whereas 21,433 randomly selected grade cows averaged 7,728 lb. of milk testing 4.12, or 319 lb., of butterfat. It is sometimes argued that the grades are practically as good as the purebred and the fact that the grades so often owe their desirable qualities to the "blood" of registered animals is entirely overlooked. In commercial production, grade animals will probably always fill a very important place, but they will probably continue to depend on the purebreds for their improvement.

TABLE 4.—AUCTION-SALE PRICES OF SOME CLASSES OF PUREBRED LIVESTOCK

	1920	1924	1928	1932	1936	1940
Ayrshire	$359	$124	$184	$108	$156	$146
Guernsey	508	380	365	162	252	225
Holstein	372	192	218	105	164	173
Jersey	354	206	211	126	161	147
Aberdeen Angus	705	150	170	106	161	209
Shorthorn	603	160	192	104	137	171
Chester White	90	65	55	35	45	50
American and Delaine Merinos*	35	35	35	15	25	30

* Estimates.

Table 4 shows the average auction-sale prices of some classes of purebred livestock for the period 1920–1940.

The value of purebred animals is forcibly brought out by the foregoing compilation. There can be no question but that the average purebred animal is a more efficient and more valuable animal than the average grade animal, though like all other rules this one has its exceptions. An educational movement to promote greater interest in better flocks and herds was taken in 1919 by the U.S. Department of Agriculture in the "better sires—better stock" campaign. Up to Apr. 20, 1941, there had been 18,490 enrollments in this activity, which is promoted largely by the county agricultural agents. Several counties in the United States are now entirely free from grade and scrub bulls. More recently many states have inaugurated "proved-sire" or "record-of-performance-sire" campaigns that are meeting with signal success.

Most of our purebred breed associations in the United States were formed about 1875–1885. Importations of purebred livestock into this country preceded this, to be sure, but it was given great impetus by the formation of the breed associations. Table 5 shows the number of animals of different breeds that have been registered up to the present.

Foods of Animal Origin.—A rapidly increasing population does not necessarily mean the extinction of any particular class of livestock. It should, however, mean the rapid passing of inefficient members of all classes. Thickly populated European countries still produce meat, milk, wool, and power, and the actual number of animals in the United States is still increasing. This, together with the animals' increasing productivity, means that our population is consuming more animal products than ever before. The population of the United States was about 5 million in 1800 and has grown to about 132 million in 1940. It has been variously estimated that the total population that can be provided with home-grown food in the United States is 200 up to 331 million and that this saturation point will be reached in 25 to 50 years.* This is based on maintaining the present dietary standard. The average per capita consumption of dairy products is still far below the nutritional optimum, for our people consume on the average about 1½ glasses of milk, ¾ oz. of butter (3 pats), ¼ oz. of cheese per person per day, and about 1 dish of ice cream per person per week. In addition there is an average consumption of about 1 can of evaporated milk per person every 3 weeks plus a small amount of sweetened condensed milk.

The present per capita consumption of meats is as follows: beef 60 lb.; veal 7 lb.; lamb 6 lb.; pork products 67 lb.; a total of 140 lb. per capita per year. This is lower than it is in several countries, higher than that in many other countries. Whether or not it is the optimum the writer does not know, but he is confident that meat would be in greater demand

*Latest estimates are for our peak population to reach 153 million in 1980.

TABLE 5.—NUMBER OF REGISTRATIONS IN THE VARIOUS PURE BREEDS*

	Membership	1940 registration	All-time registration	Year formed
Cattle Associations				
Hereford	8,295	191,624	3,294,374	1882
Holstein-Friesian	32,000	145,423	3,082,514	1885
Shorthorn	9,076	41,674	2,737,207	1882
Jersey	1,518	49,875	1,720,158	1868
Guernsey	2,240	57,796	981,067	1877
Aberdeen Angus	7,500	31,788	630,720	1883
Ayrshire	4,701	16,237	311,880	1875
Polled Hereford	1,130	10,080	151,700	1900
Red Polled	745	2,075	149,673	1889
Brown Swiss	1,250	11,161	144,315	1880
Milking Shorthorn	3,300	14,665	91,270	1920
Devon	100	282	29,489	1880
Horse Associations				
Percheron	6,140	2,759	239,900	1876
Trotting	......	2,500	225,000	1871
Thoroughbred	......	6,559	75,000	1868
Belgian	4,500	2,379	54,300	1887
Saddle	319	2,732	50,749	1891
Jack and Jennet	2,088	552	30,836	1888
Shetland	653	212	22,325	1890
Shire	587	45	21,770	1885
Morgan	147	311	13,964	1909
Hackney	101	100	7,300	*1890
Tennessee Walking Horse	360	1,220	5,148	
Suffolk	50	78	2,239	1911
Arab	155	175	2,020	1908
Welsh	51	3	1,124	1906
Palomino	......	100	900	
Sheep Associations				
Shropshire	10,500	25,000	942,000	1884
Hampshire	4,300	28,120	526,880	1889
Rambouillet	1,693	12,596	420,522	1889
American and Delaine Merino	500	5,079	315,326	1906
Oxford	1,250	3,375	169,155	1882
Southdown	665	8,350	125,596	1882
Cotswold	150	664	123,212	1878
Lincoln	400	2,000	75,000	1890
Cheviot	350	1,600	40,000	1900
American Corriedale	99	2,847	23,373	1916
Romney	130	1,363	16,000	1911
National Corriedale	292	2,528	13,465	1915
National Suffolk	75	1,409	6,711	
American Suffolk	66	2,250	5,643	1911
Swine Associations				
United Duroc	3,000	31,973	1,973,986	1883
Standard Poland China	953	....	573,362	1887
Chester White	3,451	10,622	523,222	1884
Hampshire	5,526	17,958	461,635	1893
National Spotted Poland China	9,100	15,000	440,000	1912
Berkshire	4,062	18,428	425,450	1875
Ohio Improved Chester	2,228	4,595	162,703	1897
Yorkshire	125	380	40,540	1893
National Hereford	268	4,515	9,097	
Goat Associations				
American Milk Goat record	500	3,786	65,565	1904

* New England Homestead, Springfield, Mass., Sept. 6, 1941.

if the means for its purchase could be made available. In terms of the 21 meals that most of us eat each week, our present consumption of meat would provide about as follows: for 3 meals we could have 7 oz. of beef and veal; for 1 meal we could have 1.9 oz. of lamb; and for 3 meals we could have 7 oz. of pork, leaving 14 meals each week without any meat. Or the 43 oz. of meat we consume on the average each week would give us 1 serving of about 8 oz. for some meal on each of 5 days of the week, leaving 2 days without any meat.

It would be possible to maintain a much larger population on primary food products (grain, etc.) because of the unavoidable losses in all animal feeding and the fact that no return is received from that portion of the animal's food which goes for maintenance and which amounts to approximately one-half. The inclusion of animal products in the diet, however, makes it much easier to provide a balanced diet with all the necessary nutritional elements, including minerals and vitamins, plus the additional important fact of making the diet, to most of us at least, much more palatable and enjoyable. Much energy is stored here on earth in a form not suitable for human consumption, and there is the added consideration of soil productivity, both of which make animal raising indispensable.

The following graph shows the trends in the number of different animals per capita in the United States during the past 60 years.

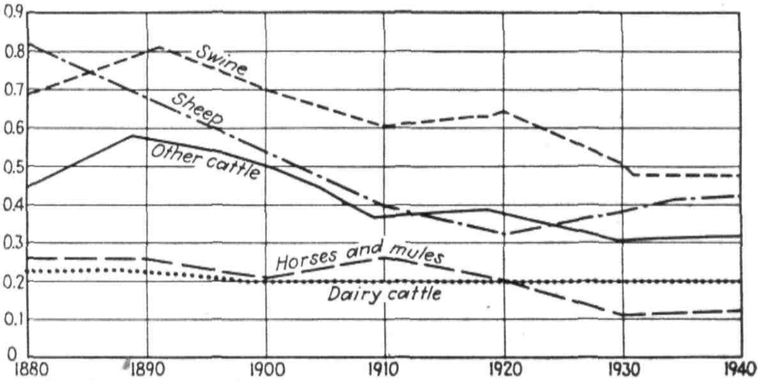

FIG. 1.—Graph showing number of various classes of livestock per capita in the United States, 1880–1940.

Table 6 gives a picture of the trend in meat consumption per capita in the United States since 1900.

The trends indicated by Fig. 1 and Table 6 certainly do not mean the passing of animal foods from our dietary. Nevertheless, they should mean the rapid passing of inefficient animals, of which there is a goodly share at present. Meats are palatable and nutritious and will

TABLE 6.—MEAT CONSUMPTION PER CAPITA, UNITED STATES
In Pounds

Year	Beef	Pork*	Lamb	Veal	All meats
1900	68	65	6.8	3.5	143
1907	77	64	6.4	6.7	155
1917	60	50	4.6	6.5	120
1930	50	68	6.6	6.8	132
1931	50	70	7.1	6.9	133
1932	47	72	7.1	6.8	133
1940	60	67	6.0	7.0	140

* Excluding lard.

be utilized as long as they can be secured and paid for. At the present time, milk would seem to be an indispensable article of diet and Fig. 1 shows that dairy cattle are maintaining their numbers in relation to population. If they are increasing in average yield of production, there is certainly no less milk being consumed per capita by an increasing population.

Dietary standards, coarse feeds, and climatic and soil conditions would seem an effectual barrier against the passing of livestock. Increasing population means an increased demand for food of all kinds; hence no time should be lost in raising the efficiency of food production to the highest possible level. In such a program there will surely be found a place for all of the really efficient animals that can be produced.

Present Status and Problems.—Many animals are unprofitably low or inefficient producers because they are poorly fed and cared for. If the average horse were well fed and cared for and were thus able to work and breed at maximum efficiency, if the average cow, ewe, and sow were performing at somewhere near the maximum set by their inheritance, livestock farming would be much more profitable than it now is. This involves also the control or elimination of our various and sundry livestock pests and diseases, which take an annual toll of millions of dollars in terms of lowered individual and breeding efficiency. Likewise our civilization would be on a much higher plane if each individual were performing more closely to his inherited capacities. The problem facing us, therefore, as far as our animals are concerned, consists of using what we have more efficiently as well as raising the level of capabilities through selective breeding.

In one sense a treatise on the breeding and improvement of farm animals seems rather futile without its corollary, the breeding of better men, for, if our human inheritance and environment were better and we could induce our people to live and work more nearly to the upper limit of their capabilities, there would be less need to write books about breeding

better livestock. An encouraging angle, however, is the fact that the principles underlying the creation and maximum productivity of livestock are identical with the principles underlying these things in man himself. If we can put the principles to work generally with our livestock, they will perhaps gradually become incorporated in our thinking about ourselves.

In our animal breeding we must, of course, start from where we now are with what we have inherited from the past. The genetic task in the field of breeding, therefore, is twofold: first, to find out what we have genetically, in other words, to analyze; and, second, to raise the average

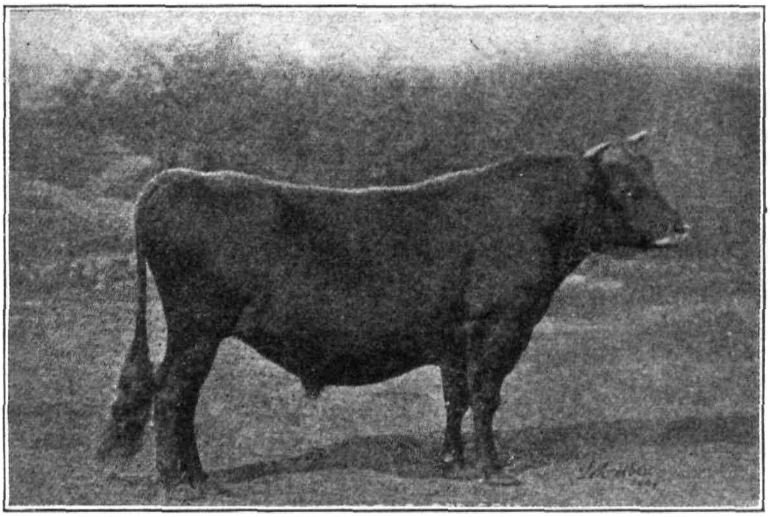

FIG. 2.—Merry Maidens 3rd Son. One of the two Jersey bulls at the head of the demonstration herd at the St. Louis Exposition, 1904.

level of production and efficiency all along the line by making better combinations of genetic materials, in other words, to synthesize.

There can be little question about the fact that most of our animals at the present time are mixed in their inheritance. We shall learn later that inheritance is due to the actions and interactions of discrete bodies called *genes* which are found associated in groups, each group of genes being called a *chromosome.* The chromosomes (*chroma* the Greek word for color, and *soma* the word for body) are found in the nuclei of cells. Each species of plant and animal has a definite, permanent number of chromosomes. If a member of the Shorthorn breed of cattle got the gene, or determiner, for red color (R) in a chromosome from its sire and the gene for white color (W) in a chromosome from its dam, its genetic make-up would be RW and its color would be roan. Such an animal

cannot breed true because it will pass along to each of its offspring either the chromosome containing the gene *R* or the one containing the gene *W*.

This illustrates the two basic concepts of modern breeding knowledge: first, the mechanism of inheritance is found in discrete bodies (genes) or, in other words, is particulate; and, second, each offspring gets only one-half of the genetic material which its parent possesses, in other words, the inheritance is halved each time it is passed to an offspring. So an *RW* (roan) animal cannot breed true because it cannot give an identical gene (in this case determiner of color) to all of its offspring. This animal is not pure for color, speaking genetically, or, in technical terms,

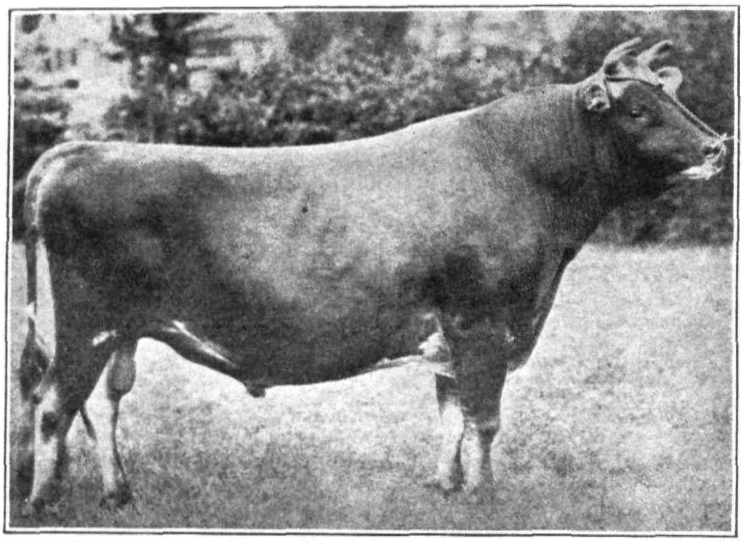

FIG. 3.—Ferns Wexford Noble, Grand Champion Jersey Bull at National Dairy Show, 1922, 1923, and 1924. A son was grand champion in 1925 and another son was junior champion.

is *heterozygous* as far as color is concerned. An *RR* or a *WW* animal is pure genetically (for color) or, in technical terms, *homozygous* (for color) and will, therefore, breed true in the sense of passing an identical gene to each of its offspring.

Our breeds of livestock are pure, or relatively so, for certain distinguishing color markings, for horns or for no horns, etc., but they are not pure for the genes that determine commercially valuable characteristics. They have been made pure or homozygous for their superficial trade-marks by the simple process of weeding out those animals which were themselves not pure as evidenced either in their own make-up or in that of their offspring.

They are not pure for speed and stamina, rapidity and efficiency of gain and quality of carcass, quality and quantity of meat and wool.

amount and quality of milk, etc., simply because we have not yet ruthlessly culled out those which do not measure up to a given standard. We have all sorts of shapes and qualities and productiveness in our livestock, and they cannot yet be counted on to transmit as they themselves look or behave. They are heterozygous in their genetic make-up and hence cannot breed true or uniformly.

The greatest need in animal breeding today is for records of performance so that we may learn definitely how our animals are transmitting. When these are available, we can intelligently weed out the unfit, breed only from the fit and so, gradually, purify our stock in terms of their commercially desirable characters.

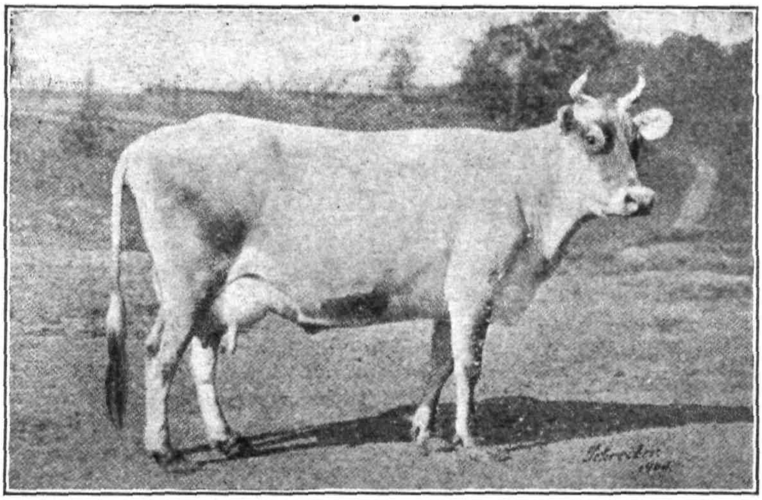

FIG. 4.—King's Gazelle Fawn, one of the Jerseys in the St. Louis Exposition breed test, 1904.

Breeding Opportunities.—Although it cannot be denied that wellnigh perfect specimens of the various classes and breeds of livestock have been produced and that in practically all breeds the prices paid for individuals have risen well into the thousands of dollars, the fact remains that opportunity is still written large before animal breeders. A few nearly perfect specimens have been produced and record after record has been established only to be replaced by a better one after a short while.

The record in milk production during 1 year is 41,943 lb. (Carnation Ormsby Madcap Fayne, H. F.), in butterfat 1,614 lb. (Melba 15th of Darbalara, Milking Shorthorn), in speed at the trot for 1 mile, 1 minute 55$\frac{1}{4}$ seconds (Greyhound), at the pace, 1 minute 55 seconds (Billy Direct). New world's records in horse pulling contests, both in light and heavy classes, were established at Hillsdale, Mich., Sept. 24 and 25,

1940. The new record for heavyweight teams is 4,025 lb. tractive pull, which is equivalent to starting a load of 52,272 lb. on a wagon on granite-block pavement 15 to 20 consecutive times. The new record for light-weight teams is 3,275 lb. tractive pull, which is equivalent to starting a load of 42,532 lb. on a wagon on granite-block pavement for the same number of times. The record in the ton-litter contest stands at 5,117 lb., the combined weight attained by an Illinois litter of 17 pigs in 180 days.

The outstanding Rambouillet sire, Prince of Parowan, owned by the Bureau of Animal Industry, produced seven annual fleeces of wool that averaged 31.5 lb. per fleece, unscoured, an outstanding record of long-

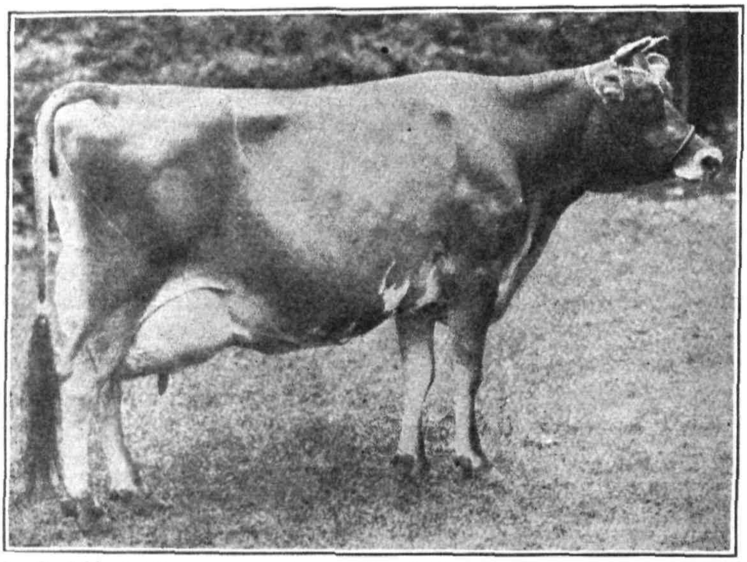

FIG. 5.—Sociable Sybil, seventeen times a Grand Champion Jersey cow, including the National Dairy show, 1923.

time wool production. This wool yielded about 40 per cent of clean wool or 12.6 lb. of actual wool per fleece. A large percentage of several hundred of the best Rambouillet sheep in the flocks of the Western Sheep Breeding Laboratory, Dubois, Idaho, are descendants of this ram. The record in wool production is a fleece of 52 lb. from 12 months' growth.

The ability of the goat to produce milk is evidenced by the fact that the highest official test on record in the United States was made by a Saanen doe that produced 4,161.7 lb. of milk in 9 months and 10 days, an average for the period of 6.9 qt. a day.

An idea of the opportunity for improvement within a particular breed of beef cattle by breeding and selection may be gained from some of the

Bureau of Animal Industry record-of-performance data with steers, which show a range in efficiency all the way from 12.01 to 20.91 lb. of live weight gained for each 100 lb. of total digestible nutrients consumed.

During the bureau's work on the development of a high level of milk- and beef-producing ability in dual-purpose cattle, one of the cows as a senior two-year-old produced 7,861 lb. of milk and 317 lb. of butterfat in 365 days on two milkings a day, the milk testing 4.04 per cent. This cow had two daughters whose records were as follows: daughter No. 1 as a junior three-year-old produced 6,017 lb. of milk testing 4.08 per cent with 245 lb. of fat in 365 days on two milkings a day; daughter No. 2 as a junior two-year-old produced 6,574 lb. of milk testing 3.96 per cent with 260 lb. of fat in 365 days on two milkings a day.

FIG. 6.—William Duthie of Collynie, a Shorthorn breeder who held annual sales for 39 years and sold 1,022 head, mostly bull calves, for a grand total of $1,238,646. (*Courtesy Breeders Gazette.*)

A steer out of daughter No. 1 in a record-of-performance test displayed an efficiency of 15.99 lb. of live-weight gain per 100 lb. of total digestible nutrients fed. The range in efficiency displayed by steers of this breed spread from 10.53 to 20.70 lb. per 100 lb. of total digestible nutrients.

All these records, when compared with the average performance of our livestock, indicate the tremendous opportunities still existing in the field of breeding. These top-notch animals resulted from certain combinations of hereditary units plus, of course, excellent care, feeding, training, and general management. As we shall learn later, there are literally billions of ways in which the hereditary units can be combined. Our first job is to learn the true nature of these hereditary units in our livestock through careful record keeping and then to recombine the units into more desirable combinations through systems of breeding and selection.

Breeding is the improvement of animals through rational selection of germ plasm and full development of resulting somatoplasm. A cursory glance at the qualifications requisite in one who is to improve animals removes at once any surprise at the scarcity of such breeders. Men like Bakewell, Cruickshank, Col. Taylor, Lothrop Ames, Gentry, Duthie, Marsh, and a score of others of greater or lesser fame are, com-

paratively speaking, very rare because of the size of the task and the multiplicity of details with which a breeder must deal.

Successful breeders are equipped with keen powers of observation, are thorough students of animal form and function who are able to select and mate wisely, are good farmers and intelligent feeders who can bring to full expression the inherent potentialities of their animals, and they are not deficient in business acumen, which makes possible the accumulation and wise use of capital. They are the type of men who inspire loyalty and fairness from those with whom they come in contact. In short, successful breeders are usually hard-working practical idealists who appreciate the privilege of working with the Creator in molding nature's forms more closely after some ideal by means of records of performance, systems of breeding, and selection.

The Purebred Era.—The rise of the present-day pure breeds of domestic livestock dates back a comparatively short time. Practically all of them arose during the eighteenth and nineteenth centuries. A few breeders saw the desirability of intensifying the "blood" of outstanding individuals when they appeared and dared, in the face of popular fear and disapproval, to inbreed to achieve their ends. Their methods proved efficacious, though it is quite certain that these early breeders could have advanced no scientific explanation for the results obtained. In terms of genetics they took a very heterozygous strain, inbred it, which sorted it out into homozygous form, and then disposed of those undesirable animals which no doubt carried double sets of recessive factors. Such methods are still efficacious, but it is a question whether or not they are being used as much as they might well be.

The term *purebred* may in some instances be something of a misnomer. For example, the term *purebred dairy cow* should imply, it would seem, that the animal in question is capable of producing large quantities of milk. It does not, of course, imply anything of the sort but only that the animal's sire and dam were purebred. Our dairy breeds are relatively pure for color, size, etc., but they are not yet pure for high milk production, though, of course, by proper methods of selection they can be made so. It would be much better to speak of these animals as *registered* rather than as *purebred* and to use this latter term only in its genetic sense. The term *purebred*, however, has gained a place through common usage that it would be futile to oppose. The student, nevertheless, should be on his guard and cognizant of the various shades of meaning of the term *purebred*.

The first herd book, for keeping Thoroughbred pedigrees, was a private affair started in England in 1791 to be followed by another private herd book for Shorthorns in 1822. None of our purebred registry associations in the United States is as yet seventy-five years old. Pedi-

grees for the Thoroughbred horse and the Jersey cow were first kept in America in 1868, for the Corriedale Sheep in 1915. There were 11 of the more important breed associations formed in the decade 1870–1880; 13 in the next decade, 1880–1890; 6 in the next, 1890–1900; 2 in the next, 1900–1910; and 3 in that from 1910–1920. The average date for the founding of the cattle associations was about the year 1870, for horse and swine associations about 1880, and for the sheep associations about 1890.

Men with common interests in the same breed of livestock banded themselves together into breed associations for two prime reasons. One of these was to protect the purity of the breed in order that it might retain its distinctive external trade-marks or to keep out the genes that determined characters not wanted. This was to be accomplished by a system of registration open at first to animals that met these certain trade-mark qualifications. This practice in due time was to be superseded by the stipulation that only the offspring of registered animals were to be eligible for registration. Because no stipulations regarding ability to fatten or to milk, etc., were or ever have been set up, it is not to be wondered at that poor producers were originally admitted into the select circle of the purebreds and are still to be found there. For many years any horse could be admitted to the Standardbred Register for horses on successfully meeting certain requirements for speed. The only criterion for the admittance to registration of a calf of the dairy breeds is that its sire and dam be registered animals. In the one case the criterion was performance with no questions asked about parentage. In the other it is parentage with no questions asked about performance. Perhaps the first system was wrong, certainly the second is, and the best system would include stipulations regarding both performance and pedigree.

Some of the breed associations, having realized that much poor germ plasm is to be found in all breeds, are now struggling to devise means of selective registration. Rules that will be genetically sound and commercially fair as well as practicable for this sort of thing are very difficult to formulate. If the difficulties prove insurmountable, an alternative method would be something similar to the herd test in the dairy breeds. In this system every female in the herd must be tested, *i.e.*, her milk weighed and its butterfat percentage determined. If this practice could be made widespread and all the facts published, the breed would gradually purge itself of its poor germ plasm, assuming that no dairyman would use a son of a bull which had demonstrated his own lack of the genes for high production through the low production of his daughters. Such a system is very slow, perhaps too slow, and a bull may have many daughters as well as many sons in service before his own poor inheritance has had time to show itself in the first 5 to 10 daughters' production.

The other prime function of the breed associations was that of promoting its particular breed. This led to some very worth-while competition between the breeds and some, perhaps, that was not very much worth while. Much of this early breed-promotion work was based on superficialities, largely perhaps because the real basis for animal improvement was at the time unknown. Excessive fat was utilized to produce even contours, cows were forced to abnormally high and probably uneconomical milk production in order to "sell" the breed. Breeds were judged, by the unthinking, in terms of a few superlative accomplishments rather than in terms of their average level of merit. Demand for purebred sires was very brisk with the result that every breed retained much poor germ plasm, and a lot of it is there to this day. To get a purebred sire seemed to be the easy and quick way out of all our breeding

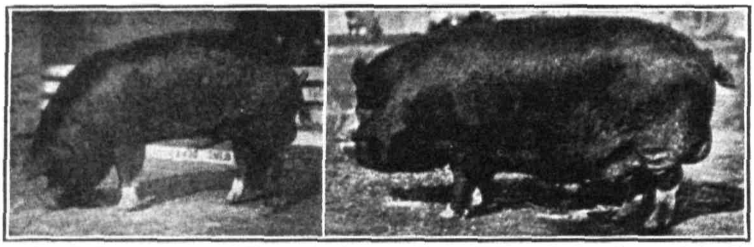

FIG. 7.—Different types of Berkshire boars. Left, Willow Lodge Baron 8th, Grand Champion International, 1923; right, Pearl's Successor 8th, Grand Champion, Eastern States, 1920.

difficulties. This attitude is found in all fields of human endeavor. We want to get to our goal by a quick and easy method, so we take various and sundry short cuts, but, unfortunately, they seldom or never lead us to our goal. Breeding better livestock is a slow, tedious process. If we use proper methods, we can hope to make some progress; but we should beware of short cuts and panaceas.

The breed associations also set the ideals for their breeders largely through the awards made at livestock shows. The breed associations have always exercised their right to have something to say about who shall judge at livestock shows. Many of them publish lists of acceptable judges, and some of them conduct judging schools to train judges in breed ideals and to encourage uniformity in placings in different sections of the country. In brief, they try to mold their breeds after acceptable standards of perfection. In all this up to the present, there has been no compulsion. Each breeder is free to follow his own bent, to test or to show or not to do so. Any breeder is free to attempt to change the presently accepted breed type and the types have been changed many times, presumably in accordance with changing market demands.

Our purebred breed associations have made invaluable contributions to better livestock. That they should not have made mistakes would have been miraculous. Their good far outweighs the bad up to the present, but they still have much hard work to do. Their final task will consist of providing the mechanism for proving the producing and transmitting merit of the animals in their respective breeds. When they add proving to protecting and promoting, they will have entrenched themselves beyond the peradventure of dislodgment by any system of crossing breeds.

The title of this section, "The Purebred Era," should not be construed as meaning that the writer believes the purebred has had its day and will pass on. The work of the purebred breed associations over the past 75 years has laid a firm foundation on which a great superstructure of really beautiful and efficient animal types can and will be built. It has been our purpose to pay our respects to the untiring work that the men making up these associations have done and also to point out the ultimate fallacy of protecting breed purity and promoting the use of purebreds without taking the necessary steps to purge the breeds of their undesirable germ plasm by feasible systems for proving breeding merit.

That genetic variations in efficiency in converting feed into milk, butterfat, meat, wool, or power exist among our animals is now well-established through carefully controlled experimental work. Probably there are also genetic differences in disease resistance, maternal characteristics, quality of product, fertility, ease of milking, etc. The next task of the breeder and breed associations is to devise the recording machinery so that these inherited differences may be ascertained and the facts made available to all.

Rise of the Breeds.—For 200 years after the beginning of the settlement of North America, the early settlers and later immigrants brought livestock to these shores, as none of the larger farm animals were here when they came. These were the native stock of their respective native lands. There were no breeds as we use the term today, although local varieties of animals have probably been continuously developed in all parts of the world for the past few thousand years. Certainly that was the case in early America, and some of these creations have persisted and developed into well-established breeds.

The early settlers needed transportation, especially when the country began to expand westward, and naturally turned to the horse. Through selection there was gradually developed a sturdy, sure-footed, intelligent, and easy-riding horse that was later to provide one of the foundation stones for the American Saddle Horse, the latter breed also having infusions of Thoroughbred, Morgan, and Trotting blood. The need for a means of travel was met in a practical matter-of-fact way, and to these

basic fundamental traits were added later the refinements of form and style to make one of man's finest creations, the American Saddle Horse. The story can be repeated for the American Trotter and Pacer, for the Chester White, Duroc-Jersey, Poland China, and Hampshire breeds of swine, and for a few breeds of sheep, whereas none of our present breeds of cattle is entirely of our own making.

We have seen that the mean date for the founding of our livestock breed associations in America was about the year 1880. This was preceded by a period of about 50 years of final preparation. The average mean date for the introduction from other parts of the world of the local varieties of horses that later became recognized as distinct breeds was about 1820, for cattle 1830, and for sheep and swine 1840. During the years from 1830 to 1880, when the breed associations were formed, strains of red, black, white, belted, or spotted hogs were developed; likewise, strains of trotting, saddle, general-purpose, and draft horses; of black, red, black and white, red and white, light or dark-fawn cattle; and of sheep of varying sizes and qualities of meat and wool. Through a gradual process of selection, involving both external trade-marks and intrinsic abilities to render some sort of service to man, the stage was set for the formation of breed associations, each group of men with somewhat similar likes and ideals banding together so as to be able to trace pedigrees more accurately and to merge their efforts of promotion.

All of our breeds, foreign or American formed, are of relatively recent origin. All of them arose by the same process of choosing certain contributions of characters from the general inheritance that makes up cattle or horses, swine, sheep, goats, dogs, etc. Our breeds arose from a grand and glorious mixture, and as yet we have purified them only for their less intrinsically valuable qualities.

The exact origin of a breed old or new can never be accurately known. This point needs no elaboration for the old breeds. But suppose that we set out to create a new breed by crossing Guernseys and Holsteins. In the first-cross animals we would know that one-half of their genetic material had come from one breed, one-half from the other, but when we mate two of these crossbreds we have no way of telling what each one is transmitting. Assuming there are 60 chromosomes in cattle, then the hybrid has 30 each from the Guernsey and Holstein breeds, or 60 in all. Each individual, however, transmits only half of its own genetic material to each of its offspring, so that in one case the first-cross animal might transmit 15 chromosomes from each of its two original sources. It might transmit 16-14 or 17-13 or 18-12 or any combination up to 30-0, but there would be absolutely no way by which to determine what the combination was. So the exact origin in terms of genetic material for a breed either old or new can never be known.

Before the advent of breeds, it is logical to suppose that the main criterion for selection was utility. The halo attached to or developed around the term *purebred* was responsible perhaps for relegating proved merit to something less than the main criterion in selection. If this has occurred, it is a distinct loss and an impediment that should be dispensed with as quickly as possible. The breeders themselves are the ones who should take the lead in accomplishing this result.

Beginnings of Breeds in England.—During the eighteenth century, agricultural progress in England quickened. By 1700 from one-third to one-half of the arable land was still cultivated on the open-field system with its heavy hand laid against more progressive and efficient methods.

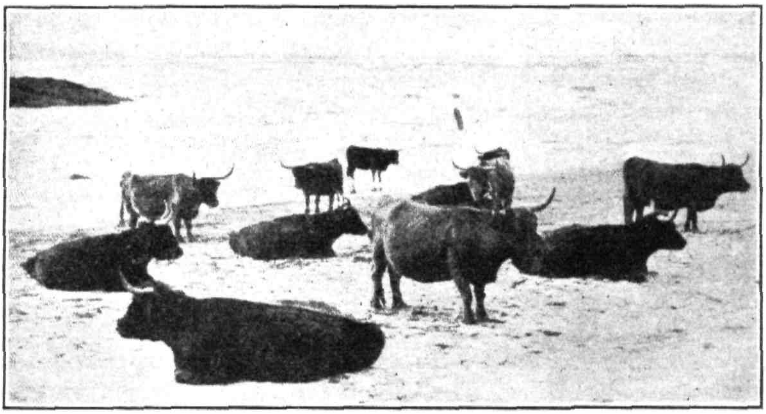

FIG. 8.—West Highland cows, of great antiquity and indigenous to Great Britain. (*From Thompson, Outline of Science, Geo. Newnes, Ltd.*)

"No individual owner could attempt to improve his flock or his herd, when all the cattle and sheep of the village grazed together on the same commons." Common lands with movable landmarks, unfenced land with crops often despoiled by passing cattle and sheep led to continuous quarreling and litigation. This type of farming was especially hard on livestock as the commons were generally overstocked. Writers spoke of "half-starved, greyhound-like sheep," of "animals bearing a closer resemblance to living skeletons than anything else," and of a motley mixture of all the different breeds of cattle and sheep at present known in the island, many of which are diseased, deformed, small, and in every respect unworthy of being bred from. It was claimed that 5 acres of individually owned pasture would have been worth more than pasture rights over 250 acres of common. Enclosing started about 1450 and progressed at different rates in different parts of England, sometimes by agreement, sometimes by acts of Parliament.

tion. This system, then as now, leads to purity or homozygosity. When other breeders adopted Bakewell's methods, the foundations of our modern purebreds were laid.

Late Middle-Ages Agriculture of England.—During the Middle Ages (500–1500) in England, as elsewhere, rotation and improvement of crops and improved breeding methods were not a necessity because virgin soil was abundant and worn-out lands could be deserted for new. Increasing population and the establishment of settlements were later to make improved husbandry a dire necessity. Thus wild field-grass husbandry was supplanted by the permanent separation of arable from pasture land. The former was the system in vogue during feudal days in England from the eleventh to the fifteenth centuries. At this time there were four types of land (1) the demense or lord's land, (2) the free land of the military service or rent-paying men, (3) the unfree land worked by various classes of bondsmen, and (4) the common pastures and untilled wastes. Each manor was self-sustaining, and there was but little trade in agricultural products. "For such ready money as he needed, the lord looked mainly to the produce of his livestock."

Horse farms appear in the accounts of some of the manors in the thirteenth century, probably supplying the "great horse" for military purposes. Cart and plow horses were to be found on most farms and were often worked along with oxen. The latter were steadier, easier on the harness and plow gear. The winter keep of oxen was less than that of horses. They needed less care, were less liable to sickness, and on death yielded both a hide and a carcass. Attendants of both classes slept in the barns with their charges.

Cattle fared badly in these early days. Pastures, never very plentiful, were generally overgrazed so that fresh-butchered meat was seldom eaten. Aged animals and worn-out oxen were prepared after a fashion through the summer for slaughter in the fall and then eaten fresh or salted for winter use. Winter feed was scarce with the result that spring generally found the cattle in a very thin and weakened condition.

Dairy cattle fared little better and produced four-fifths of their yield during the 24 weeks of summer. In the winter milk was worth three times its summer price. Not many calves were grown because of the greater human demand for milk. Much use was made of all sorts of cheeses and much summer butter was preserved for winter use.

To the medieval agriculturalist, sheep were the sheet anchor of farming. Their chief product was not meat, milk, or hides, but wool. From earliest times, districts like Shropshire, Leominster, and the Cotswolds had been famous for their wool. The high prices paid for rams is evidence of an attempt at better breeding, though the presence of scab and rot made sheep raising a risky venture. The shepherd's task was one

of the most important ones on the farm, he was respected above most others and lame shepherds were in great demand because a lame man was not likely to overdrive his sheep.

Pigs were held in high favor and valued as more profitable than a cow. They were also invaluable as scavengers. Turned loose, they were self-supporting during all except 3 months of the year. At farrowing and fattening time they received some extra care and feed. In type they were rangy, lop-eared, and agile. What selection was practiced was based largely on the animal's ability to fend for itself, "root hog or die."

To sum up the status of livestock in thirteenth-century England, we have seen that types of animals to fit the contemporary need had been developed, but that means of adequate feeding or very high ideals of better breeding were sadly lacking. Nevertheless an adage of the time ran, "He that hath sheep, swine, and bees, sleep he, wake he, he may thrive."

The open-field system, including the arable land, the meadow, and the permanent pasture land, prevailed quite generally in England at some time or other, and examples could still be found up to the eighteenth century. The manor system of farming tended to break up between 1300 and 1485, largely because the lords became more interested in sport and war than in improving farming practices. Famine followed, owing to lack of interest by the large owners and the lack of resources of lesser men. Whatever improvements were registered were largely the contribution of monks, but winter was a season to be dreaded. Gradually, and for a variety of reasons, the manor system with its graduated mutual dependence began to break up and was supplemented by a system that involved greater individual independence.

The Black Death (1348–1349) hastened the breakup of the manors as it increased the lord's land but greatly decreased the available labor supply. Rents fell, wages rose, and extensive legislation designed to aid the landlord could not stem the tide of manorial breakup. More and more small separate farms came into being that were let out for money rents to individual occupiers. Freeholders, leaseholders, renters, and free laborers increased at the expense of the class of villeins.

Thus, shortly before 1500, feudalism in England practically ceased to exist—the Middle Ages were supplanted by modern times. Feudalism was followed by enclosure. Open fields and pasture commons were enclosed, sounding the death knell to the old medieval agrarian partnerships and signifying the birth of individual ownership. The rise of a very profitable wool trade as well as the increased demand for meat turned much arable land into pasture, much of the change being unwarranted. Land now came to be thought of in terms of what rent it could earn; in other words, agriculture became commercial.

Grass holdings were enlarged at the expense of tillage in order to accommodate the sheep-farming craze. In the process many small farmers were ruined and many once happy villages became "deserted." Laws passed to preserve farm homes and buildings and to require tillage were easily circumvented and preachers and versifiers inveighed against sheep farmers and the sheep themselves. But the greater efficiency of enclosed land, owned and worked by an individual, over open land, jointly owned, gradually made itself felt and a new era of progressive agricultural development opened for England. The price for enclosing some ¾ million acres was the throwing out of work of around 35,000 persons. That there was much suffering can be assumed from the numerous rural uprisings of the time, but there were also attempts to deal fairly and adjudicate liberally.

Unaccompanied by a contemporaneous development of arable land, enclosures caused a growing scarcity of employment. Tenant farmers, copyholders, squatters, cottagers and laborers suffered alike, and the rise in the cost of living pushed many to the brink of starvation. Some individuals waxed rich through enclosure, so that the growing unequal distribution of wealth brought many abortive attempts at legislative relief for the unfortunate. Petty crimes, kidnapping, livestock stealing, and similar misdemeanors grew in the rural districts, though a goodly part of it was doubtless perpetrated by disbanded soldiers, adventurers, and other ne'er-do-wells.

During the reign of Elizabeth (1558–1603) "wool was the chief source of the wealth of traders and of the revenues of the crown" and controlled the foreign policy of England. Short wool had serious competition from the Spanish Merino. Ryeland was the preeminent short-wool breed, its center at Leominster and "Lemster ore" the equivalent of "golden fleece." The Cotswolds led the long-wool breeds with Lincolnshires close behind.

On the whole there was not much change in the sixteenth- as compared with thirteenth-century agriculture in England. Some gains were registered, *e.g.*, the greater use of iron in the implements used, but artificial grasses and roots were still unknown, hops the only new crop. Seasonable operations remained about the same with magic and superstition still controlling plantings and breeding operations. Sheep were considered the "most profitable cattle a man can have," though without turnips their full value could not be realized. Ewes were still milked and the writers of the time have "nothing to say about the improvement of breeds of cattle for the purposes that they serve." The general-utility animal was still the ideal. The combining of crop production with livestock feeding was yet to come.

Medieval Continental Agriculture.—In Western Europe conditions were chaotic following the breakup of the Roman Empire, which started in the third century and was complete by the seventh.

The work of reconstruction in Western Europe began in the eighth century. Various rulers, and particularly the Christian church, provided the main impetus. Methods and tools were crude and results in terms of effort meager, but progress was made and the hope of economic security was again revived. Thousands of monasteries were established all over Western Europe and each of them provided a nucleus for agricultural and livestock-breeding endeavors. Large herds of cattle, horses, sheep, and swine were again established, horticulture and winegrowing again came into prominence.

Even after their adoption of the rudiments of civilized living, the majority of the Celts, Anglo-Saxons, and Germans were largely herdsmen and in central Germany cattle were still a means of exchange up to the eighth century. The ratio of small animals like hogs, sheep, and goats to larger ones like cattle and horses ranged from 5 up to 9:1.

The period from 900 to 1200 saw the rise and the establishment of feudalism in Western Europe. Land at that time was practically the only capital and it came to be controlled by the ecclesiastical and military classes. Communal ownership of land had changed first to small individual holdings. These were gathered together into great blocks by powerful organizations or individuals. As the saying had it at that time, "no lord without land, no land without a lord." There were still some free men scattered about but one-third to one-half of all the land, for instance, was owned by the Church and another large percentage by powerful knights and barons. This land was given out as fiefs to be worked by slaves, serfs, half-free, and free peasants. Stated returns went to the lord and generally the workers also owed the lord or the monastery a stated number of days of work per week.

Nothing, of course, was known of scientific agriculture, and the lot of the peasant and his animals was not a happy one, a horse being worth 100 sous and a peasant 38 sous in the eleventh century. Fallowing was used in place of crop rotation and the cultivation of roots and grasses. Gradually centralized feudal states emerged, nationalism developed, and the monarchies began to revive. This led to extensive colonization all over Europe from the eleventh to the fourteenth centuries. With this came some attention to agriculture, irrigation, development of grasslands and fodder crops, and attempts to foster an empirical veterinary art and to improve livestock. Studs were set up to try to improve the horse for both war and commerce, and some sections became noted as mule-breeding districts. Cattle also received more attention from the stand-

point of meat and milk as well as draft. Small animals, however, continued to dominate, sheep taking the first rank. Millions of sheep were to be found in the Low Countries, France, and Germany as well as huge migratory flocks in Spain and Italy. There was improved cattle breeding in Scandinavia by the twelfth century and this region was exporting butter, cheese, fats, lard, and hides. The art of fattening cattle on roots and legumes was first developed in the Low Countries.

The eastern portion of the Roman Empire (the Byzantine) fared better following the crisis of the fifth or sixth centuries. For 1,000 years, it held off or quickly recovered from the onslaughts of the barbarians. It was realized that the two pillars of resistance were agriculture and military art. Through an intelligent system of agricultural colonization, hundreds of thousands of outsiders including barbarians were absorbed into this Eastern Empire. Agriculture, animal husbandry, and horticulture flourished, early Greek and Roman agricultural practices were revived, thereby creating the wealth that made this part of the world the envy of all men during the Middle Ages. In the early part of the period the land was held largely by individual owners, but by the tenth or eleventh century most of the lands had gotten into the hands of the Church or of large landholders. Slavery, however, was abolished, and the serfs were accorded privileges and rights, which stabilized rural life with the result that disciplined labor gave to the Eastern Empire its chief economic supremacy.

> The East Roman Empire thus accomplished, during the early Middle Ages, a task of supreme importance. It had received undiminished the heritage of Rome and added to it. It left a profound mark upon every kind of work. It succeeded in colonizing the Christian lands of Eastern Europe, and it civilized the barbarians, calling them to the fruitful labours of peace. It gave a powerful impulse to every form of economic activity, and carried the production of wealth to the highest point. If in the social order it only half succeeded in protecting free labour and free property against the exploitation and usurpations of the aristocratic classes, it yet suppressed slavery, and strove with all its strength to maintain the middle class, both urban and rural. Thus it placed itself in the van of civilization, whose great traditions it carried on, and it was partly to Byzantium that the West in its turn went to school to be prepared for its own civilizing mission.[1]

Roman Agriculture and Animal Husbandry.—The seven separate hills of Rome, settled at first by humble herders and hunters, were eventually drawn together into the Septimontium (League of the Seven Hills) and destined to become the ruling center of the greatest empire the world had ever known. Agriculture in the surrounding region kept pace

[1] BOISSONNADE, P., "Life and Work in Medieval Europe," pp. 60–61, Alfred A. Knopf, Inc., New York, 1927.

with the growth of the city and came to enjoy a real prosperity. The unpaid militia, consisting to a large extent of small farmers, was often called upon to protect the region from invaders, but the campaigns were seldom of long enough duration seriously to affect agricultural practice. This is not true, however, of the period from the first Punic War (against Carthage) in 264 B.C. down to the time of the death of Augustus A.D. 14. These were the times of Roman wars of expansion, and they were long and bloody. The middle-class farmer bore the brunt, was slaughtered by thousands with the result that a great deal of the property fell into the hands of a few rich owners. In addition, thousands of the conquered were brought to Rome and sold as slaves to work the land. The earlier type of Roman agriculture gradually found itself unable to compete with outlying conquered territories in the matter of supplying grain. The

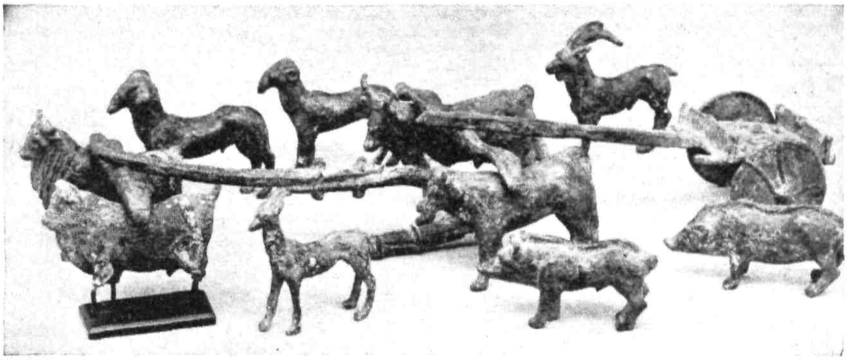

FIG. 9.—Statuettes of Roman animals in bronze, first century B.C. to third century A.D. (*Courtesy of The Metropolitan Museum of Art.*)

type of agriculture, therefore, shifted to greater numbers of livestock, especially horses, sheep, and hogs, and to increases in orchards, vineyards, and gardens. The country became almost deserted except for foreign slaves and barbarians, the drainage works fell into ruin, and the old unhealthfulness returned.

This transformation of rural economy led in the end to a social phenomenon of great importance in the history of Rome. The countryside was deserted by most of the small landowners and free tenants, who came crowding into the towns, and especially to Rome. This influx of poor people, ruined by the new conditions of farming, enormously increased the mass of the Plebeians, which was at the same time swelled by increasing throngs of freedmen of foreign origin, Greek and Oriental. There was no longer a balance in the citizen body between the rural elements, which had once been hard-working, productive, and level-headed, and the urban proletariat, which grew more and more accustomed to call upon the State, the magistrates, candidates for office and ambitious men of every kind for its food and amusements—*panem et circenses*. Rome ceased to be the

capital of an essentially agricultural people, whose wealth was mainly based on landed property and agricultural resources; it became a turbulent agglomeration, in which industry, trade, and money-dealing assumed an importance hitherto unknown.[1]

The formation of the Roman Empire near the beginning of the Christian Era brought Gaul, Spain, Africa, Greece, and Egypt under Roman influence. Rome demanded economic, political, and religious loyalty but allowed old native traditions, habits, and sentiments to persist, provided they did not interfere with the loyalties she demanded. Economic life in these conquered areas went on much as before though quickened by inclusion in a greater united whole. Roman legions and fortifications held back the barbarian hordes on all sides and gave a comparatively long period of relative peace throughout the Empire and in Rome itself, when the civil wars were extinguished.

So far as we can learn, there were no great agricultural innovations or livestock improvements either in Italy proper or in other parts of the Empire during this time. Of a slow, steady evolutionary process, however, we have reason to be assured. Selection, no doubt, went on in livestock breeding and the long period of peace during the first two centuries of the Christian Era was bound to have had its effects. We get some indication of the relative importance of various types of agriculture in the Empire from the fact that Columella's 13 books *De re rustica* include no whole book devoted to grain growing, 2½ books devoted to winegrowing, about 1 each to fruit trees, including the olive, and to gardens, while livestock occupies 4 books.

The Empire consisted of cities with surrounding agricultural lands, orchards, and vineyards. Beyond were to be found the pastoral nomads with their flocks and herds; and in the hinterland, the barbarians. Each region of the Empire adapted its crops and animals to its particular topographical and climatic conditions. Variety there was, to be sure, in lands, in peoples, in methods. Although there were large estates in all parts of the Empire worked by slaves or tenants, the real backbone of the fabulous old Roman Empire was undoubtedly to be found in the sturdy, individual small farmer, businessman, and trader. He it was who created the wealth and provided the sinews that made the Empire. When this class, for whatever reason, was forced out of existence, the "grandeur that was Rome" quickly faded.

Beginning with the third century, the power of Rome began to wane. Slowly but surely the ordered, progressive life in a well-tended countryside and in hundreds of cities with fine public buildings, temples, and

[1] Toutain, J., "The Economic Life of the Ancient World," p. 234, Alfred A. Knopf, Inc., New York, 1930.

homes was undermined by anarchy, insecurity, and discord at home and by successive waves of barbarians from the north and east. Imperial edicts proved a poor substitute for the individual efforts of free men. Thus the structure of the Empire was weakened from within and rendered highly vulnerable to attack by tribes of vandals which gloried only in destruction, murder, and rapine. So thoroughly did they carry out their mission of destruction that by the seventh century a once productive countryside had largely reverted to waste, the once proud cities were in ruins, and the population cut in half. There was barely enough courage and initiative left to start the long, tedious process of rebuilding, which was to consume the next 600 or 700 years. The effect on livestock breeding was particularly severe. Herds and flocks were wantonly destroyed and their half-starved remnants turned back to a state of nature.

Grecian Agriculture and Animal Husbandry.—Before the time of Alexander, agriculture and stockbreeding was one of the chief sources of wealth in Greece and her colonies. Their stables and byres contained horses, cattle, sheep, swine, and goats, which provided food, clothing, milk, and power. These early Greeks also kept bees, and the poultry yard contained geese, ducks, guinea fowl, and pigeons as well as hens. These people also consumed various and sundry products of the field, grains, vegetables, and fruits, and their banquets and religious ceremonies called for the liberal use of wine. In the early days of Greece, the standard of value was measured in terms of cattle, and among the prizes suggested by Achilles for the funeral games in honor of Patroclus were, besides mares and mules, a tripod valued at 12 oxen and a slave girl valued at 4 oxen. There was considerable barter involving the exchange of cattle for metals. The Greek poems of the period contain many references to wealth reckoned in terms of flocks and herds, just as in later Roman times the word for money, *pecunia*, was derived from *pecus*, cattle. The earliest known Greek coins date from the seventh century B.C.

Economic activity at this time was mainly agricultural and pastoral, pursuits which provided most of the wealth. Through the period from the eleventh to the fourth centuries B.C., some improvements in details of agriculture and animal husbandry are recorded but there was no radical change in agricultural equipment or methods and no evidence of any marked development in stockbreeding practices. Much of the work was done by slaves, though there were also individual farmers who owned and operated their farms as well as some farms that were run by hired labor.

When Alexander of Macedon led the Greeks to the conquest of Asia Minor and Egypt, a new and rich agricultural economy fell under Greek domination. Here they found a flourishing livestock industry: 30,000

mares with 300 stallions in one stud in Syria, large herds of camels farther east between Syria and the Euphrates Valley. Great herds of oxen and horses were found in the well-watered districts from the Mediterranean to the Black Sea with flocks of sheep in the higher plateaus. Even greater agricultural and livestock wealth awaited them in Egypt in spite of the misrule of the Persians during the two preceding centuries. Egypt now became the granary of the Mediterranean world in addition to supplying countless other vegetable and aromatic products as well as fruits.

FIG. 10.—Statuette of Greek horse in bronze, fifth century B.C. (*Courtesy of The Metropolitan Museum of Art.*)

Livestock too abounded in Egypt: horses, cattle, sheep, goats, poultry, of various sorts, and the real beast of burden, man's fellow worker in the fields and on the roads, the lowly ass. In addition Egypt supplied all sorts of wild game, gazelle, antelope, wild ox, goat, hare, hyena, lion, hippopotamus, crocodile, and various waterfowl. Thus a whole new world was opened up by the Greek conquest. There were huge temple properties and royal domains in both Asia Minor and Egypt, the former apparently worked by slaves and the latter by royal farmers, who were somewhat of the nature of serfs and tenants, as well as by salaried workers. In addition, there were large estates worked by tenants and probably some small, free landholders. Greek agriculture and animal husbandry

certainly took on a greater diversity during the centuries that saw Greek influence spread to Asia Minor, Syria, and Africa, but there is little evidence of any marked improvements in the techniques of either. Beneficial variations were no doubt seized upon and in some cases maintained or increased, but the general level of accomplishment in stock-breeding remained about where it had been.

Oriental Agriculture and Animal Husbandry.—Colored drawings on the walls of the tombs clustered around the Pyramids of Giza depict the life of the people who lived in Egypt about 3000 B.C. The lord of the

FIG. 11.—Wall painting of Egyptian bull during XVIII dynasty, about 1400 B.C. (*Courtesy of The Metropolitan Museum of Art.*)

estate is pictured looking out over his fields, the oldest agricultural scene now known. Cattle are shown being used to pull a crude wooden plow; others are shown grazing in pasture and still others being milked (after their hind legs had been tied to prevent kicking). Donkeys too are much in evidence, but the horse was apparently unknown to the Egyptian at this time, not appearing there until about 1700 B.C. At the Plain of Shinar, later known as Babylon, carvings and drawings from about the same time show oxen at the plow, sheep and goats at pasture, and donkeys pulling wheeled carts and chariots, the wheel appearing here for the first time. Horses made their appearance in Western civilization about 2000 B.C., when they were brought to Babylon by the conquering mountain Kassites, who in turn had gotten the domesticated horse from tribes to the north and east. To the north of Babylon was another early

civilization, the Assyrian, with its capital at Nineveh. These people too had herds of oxen, sheep, and goats and used donkeys for draft purposes. They also had domesticated horses which, together with their weapons of iron, they used very effectively in their conquests of neighboring regions. The peoples who made the Babylonian, Assyrian, and Chaldean empires came largely from the grassland fringes of the Arabian desert.

In the north was a second fount of nomadic conquerors located in the grasslands stretching from the lower Danube along the north side of the Black Sea through southern Russia and into Asia. This was a white race called Indo-European, and most of the people who will read this

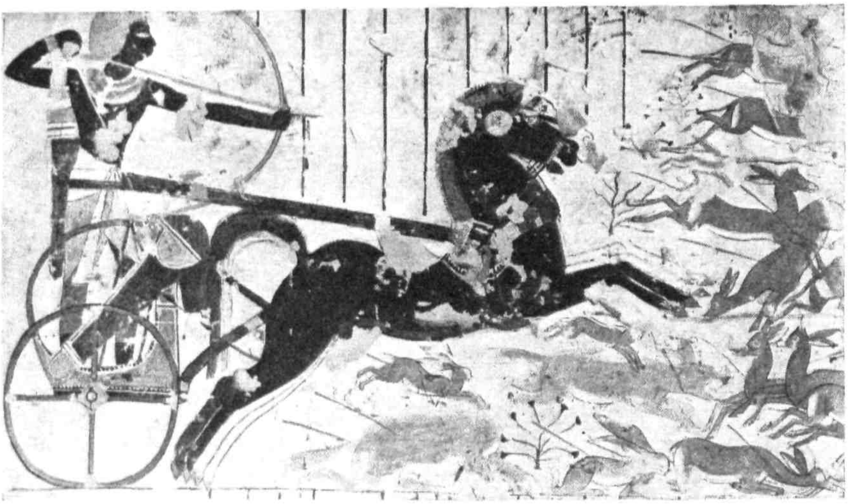

FIG. 12.—Wall painting of Egyptian hunter during XVIII dynasty, about 1400 B.C. (*Courtesy of The Metropolitan Museum of Art.*)

book are their descendants. Their original home was the grassy steppe east and northeast of the Caspian Sea. They were nomadic tribes following their flocks and herds on horseback and using horses for draft. These people were the ancestors of the Greeks and Romans and of most of the peoples of Western Europe and America. Their language group is Aryan, which includes English, German, Latin, Greek, old Persian, and East Indian although these people themselves were without writing. The Medes and the Persians were but the Eastern wing of this movement of original Northern nomads.

Here the historical record fades out. What preceded it in the field of agriculture and animal husbandry can only be surmised from occasional relics. This historical record we have traced backward from the present, a period covering about 5,000 years. We have noted some progress,

but the tempo of change was very slow. We are perhaps justified in assuming that the period from the earliest domestication of animals up to this beginning of the historical record occupied a much longer time.

Summary.—We have tried in this chapter to start from the known facts about our livestock situation of today and trace it backward to its historical beginnings. In these few pages we have covered 5,000 years of man's struggle from barbarism to a certain state of civilization. Much was accomplished, but a vast deal more still remains to be done. Without any sure knowledge, except what he could observe in the gross, man has made tremendous strides forward in breeding better livestock, aided materially of course by better housing and management and especially by better feeding. For marked progress in animal breeding we need knowledge of principles, ideals, and good feeds together with peace or at least freedom from invasion. All of these except the first were finally present in England during the eighteenth century, and it was there and then that the foundations of our modern breeds were laid.

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CHAPTER II

EARLY MAN AND ANIMAL DOMESTICATION

Man is a late arrival on the planet Earth. When he arrived, he found the earth already inhabited by myriad forms of living things. He was apparently just another in a long series of creations extending back for hundreds of millions of years to the beginning of life, just another manifestation of the great stream of life that far transcends man's own immediate interests. Before him, in time, had arrived many of the other mammals as well as the birds, reptiles, amphibia, fish, and a whole host of invertebrate forms.

It is estimated that life has existed on this planet for about 1,200 million years. Up to about 500 million years ago, the only animal forms were creatures without backbones, the invertebrates. The vertebrates, animals with backbones and an internal skeleton, appeared about 480 million years ago, the first land-living forms about 350 million years ago, the mammals about 160 million years ago, *Homo sapiens* (wise man) about 25,000 years ago, and we have something of a historical record of his doings for about 5,000 years.

The record yielding the above facts is written in the rocks of the earth's crust. The time intervals are calculated on the basis of the rate of breakdown of certain rare minerals and for more recent periods by counting the annual glacial varves. Even the ancients must have sensed something of the span of time when they wrote "A thousand years in Thy sight are but as yesterday when it is past."[1] In these trying times facts such as the above should give us new courage. In a ridiculously short span of time man has made tremendous strides forward. To say, as is sometimes done, that human nature does not change is but to show one's ignorance of the facts. Present man is probably very different intellectually, morally, and spiritually from his forebears of 50,000 years ago. In a few hundred years, recent man has come largely to understand and to be the master of his natural world. True, the much more difficult task of becoming master of himself yet remains, but in the light of the accomplishments of the stream of life over the past billion years this does not seem to be an impossible task.

The first skeleton of "modern" man appears in the geological record about 25,000 years ago. Starting with *Pithecanthropus erectus* (walking

[1] Psalm 90: 4.

ape man), who dates back from ½ to 1 million years, an incomplete and rather sketchy series of prehuman forms runs on down and finally emerges as modern man. Man is included in the Primates, a group of animals comprising the lemurs, monkeys, apes, and man. This does not mean that man has descended from monkeys but probably that man, monkeys, and the great apes are all offshoots of a common progenitor whose identity is still uncertain. The apes, therefore, are our cousins and not our direct ancestors.

The primates as a class are not of very recent origin, for fossil remains of the lemurs are known from the Oligocene and Eocene periods *i.e.*, 35 to 55 million years ago. It is impossible to say when the stock that was eventually to form man split off from the parent stock, though it is believed that both man and the modern apes are descendants of a common progenitor in the Cenozoic period. Neither is it known where, geographically, the split occurred, though either Asia or Africa seems the most probable, or whether there was one split or several in scattered localities.

The close relationship between the great apes and man is attested by the striking similarities in all their physical characteristics. One can easily point out differences between a gorilla and a man, but a detailed study would show very much more similarity than difference between these species. The monkeys and apes excel in certain respects—man in others. The most striking variations in man are, of course, the upright gait, which frees the hand to become a grasping, tool-making and -using organ, and the development of the brain. Man's brain is the finest creation of the evolutionary process and is not to be thought of as something supernatural, miraculous, or of sudden appearance. It is a slow, progressive development of evolution and still manifests a wide range of variation.

Early Forerunners of Man. *Pithecanthropus erectus.*—This, the ape man of Java, was discovered by Dr. E. Dubois of Holland on the island of Java in 1891. The find was made 45 ft. below the present level of the terrain in association with 27 different varieties mainly of extinct mammals but including the deer, boar, elephant, and hippopotamus. The find consisted of a skull cap, a left thighbone, two upper molar teeth, a lower premolar, and a fragment of a lower jaw and is generally dated as of early to middle Pleistocene Age. The skull cap is thick-walled and has a cranial capacity of about 900 cc., which is somewhat below the lower limit of present-day human skull capacity, and the brain gives evidence of being closer in form to the human than to the ape. The skull cap indicates a low cranial vault and a narrow receding forehead, and it has a very well-developed supraorbital ridge that is suggestive of the great African apes. The thighbone indicates an upright,

bipedal posture, and, judging from this bone, the creature stood about 5½ ft. in height. The two molar teeth are now thought to be those of an orang, although another much more humanlike tooth was found in the same stratum sometime later, which, if it really belonged to Pithecanthropus, adds another to this creature's manlike characteristics.

TABLE 7.—COSMIC OR ASTRONOMIC TIME CHART*

Eras	Periods	Time, years	Characteristic life
Psychozoic . . .	Recent	25,000	Man
Cenozoic, 4 per cent	Pleistocene	1,000,000	Ice Age
	Pliocene	7,000,000	Emergence of man
	Miocene	19,000,000	Culmination of mammals
	Oligocene	35,000,000	Modern mammals dominant
	Eocene	55,000,000	Archaic mammals, first horse
Mesozoic, 11 per cent	Cretaceous	95,000,000	First grasses; Culmination of reptiles
	Comanchian	120,000,000	First flowering plants; Giant reptiles, dinosaurs
	Jurassic	155,000,000	First birds, first mammals; First modern trees
	Triassic	190,000,000	Rise of dinosaurs
Palaeozoic, 30 per cent	Permian	215,000,000	Rise of reptiles
	Pennsylvanian	250,000,000	Rise of insects; Ferns and seed ferns
	Tennessean	275,000,000	Rise of sharks
	Mississippian	300,000,000	Rise of echinoderms
	Devonian	350,000,000	First land plants; First land animals
	Silurian	390,000,000	First lungfishes; First scorpions
	Cincinnatian	425,000,000	First corals
	Ordovician	480,000,000	First armored fishes
	Canadian	490,000,000	
	Ozarkian	505,000,000	Trilobites dominant
	Acadian	525,000,000	First shellfish
	Taconic	550,000,000	First known marine fauna
Proterozoic, 25 per cent.	. . . .	. . . .	Primitive invertebrates
Archaeozoic, 30 per cent.	. . . .	1,800,000,000	Earliest life

* LOOMIS, F. B., "The Evolution of the Horse," p. 24, Marshall Jones Co., Boston, 1926.

Whether Pithecanthropus was a direct ancestor (missing link) or just a collateral relative is still a question. At any rate, he still remains the lowest known member of the family Hominidae. Since no tools or artifacts were found associated with these bones, we can guess nothing as to the degree of culture that members of this race had attained, though it seems safe to assume that any culture they may have possessed was of a very primitive type.

Another find (by Dr. G. H. R. von Koenigswalde) was made in Java in 1936. This was the skull of an infant about one to two years of age, though the teeth, which would give the best indication as to age, were not found. The capacity and characteristics of this skull seem to place it in the Pithecanthropus group of the lower to middle Pleistocene, although some authorities would designate it as a skull of an infant Solo man of upper Pleistocene age. In 1937, Dr. von Koenigswalde found an adult Pithecanthropus skull in Java including four teeth of undoubted human form though of great size. This skull has an estimated capacity of about 750 cc. More recently a fourth specimen of Pithecanthropus was found of the same general type.

Sinanthropus pekinensis (Pekin Man).—The finding of human teeth in cave deposits near Pekin, China, in 1926 and 1927 led to further search in this region for human remains. The search was rewarded in 1929 when Dr. W. C. Pei of China found a nearly complete skull. Another skull was found in 1930, and since that time many fragmentary skulls, teeth, and parts of skeletons have been discovered. In 1936, three more skulls were discovered, including some of the facial bones. The first skull had a cranial capacity of something over 900 cc., and the capacity of the second was somewhat greater. The three latter skulls have capacities of 1,200, 1,100, and 1,050 cc., the last probably a female.

The general form of these skulls is similar to that of Pithecanthropus, the teeth are of human type and larger than those of recent man though there is still no chin. Associated animal fossils indicate that these men lived at about the same time as the Java man, *viz.*, during the middle Pleistocene; *i.e.*, 500,000 to 1½ million years ago. It seems established that the Pekin man used fire and had crude implements and tools made of chipped stone or the bones of animals. The greater brain capacity and manlike teeth perhaps place Sinanthropus a little higher in the scale than Pithecanthropus.

Eoanthropus dawsoni (Piltdown Man).—This discovery was made by Charles Dawson in 1911–1912. It consisted of several fragments of a human skull, much like that of a modern except for its excessive thickness of bone, and, in close proximity, the right half of a lower jaw containing two molar teeth. This portion of jaw is very similar to that of a chimpanzee, a creature, however, never found fossilized in England. Later

finds, near Piltdown, of skull fragments and teeth tend to confirm the once-doubted fact that the skull and jaw belonged originally to the same creature. The cranial capacity seems to be about 1,200 cc., and the forehead not only lacked the supraorbital ridge but was quite vertical. The apelike lower jaw has no chin but its jaw socket is formed as in *Homo sapiens*. A chipped flint and a large bone implement were found in the deposit that is generally accepted as being of early Pleistocene. These fossils have caused a great deal of argument among anthropologists, and it is still not clear where the Piltdown man fits in the general scheme of man's forerunners.

Homo heidelbergensis (*Heidelberg Man*).—This find, of a lower jaw, was made by Professor Schoetensach at Mauer, near Heidelberg, Ger-

FIG. 13.—Prehistoric man; Pithecanthropus, Piltdown, Neanderthal, Cro-Magnon. (*Courtesy of The American Museum of Natural History.*)

many, in 1907 in river sand 79 ft. below the present surface in a stratum that had yielded many bones of Pleistocene animals. This individual is thought to have lived 150,000 to 300,000 years ago. The jaw, while very heavy, has teeth that are entirely human. No artifacts were found associated with this jaw, so that nothing can be guessed as to the cultural status prevailing during his time. Again it is impossible to assign a definite place to this undoubted forerunner of man. It should be noticed that we have herewith used for the first time the genus name for man—*Homo*. That is to say *heidelbergensis* appears human enough to be placed in the same genus with present man—but he is not yet called *sapiens* (wise).

Homo neanderthalensis (*Neanderthal Man*).—We now reach a type concerning which something more definite may be said. First of all, Neanderthal man spread over the continent of Europe, into the Channel islands, and into Palestine. He had a well-defined flint-tool industry, used fire, probably buried his dead, lived contemporaneously with the

reindeer, wild horse, cave bear, and woolly mammoth during a time extending from 200,000 down to 25,000 years ago.

The first known Neanderthal skull was found in 1848 at Gibraltar, though it was not recognized as such or studied until 1906. It was that of a female with a brain capacity of about 1,300 cc. The discovery at Neanderthal occurred in 1856. This skull has a very low vault, heavy supraorbital ridges, and many unusual features in the arm and leg bones.

One of the most complete skeletons thus far discovered was found at the cave of La Chapelle-aux-Saints in France in 1908. This was an almost complete skeleton which had been buried in the floor of the cave. It has been studied in complete detail by Prof. M. Boule of Paris. Other Neanderthal skeletons or parts thereof have been discovered in various parts of France, Germany, Italy, Yugoslavia, Palestine, and in the Crimean Peninsula on the Black Sea. As would be expected, there is considerable variation in these skeletons, but no basis as yet exists for breaking *neanderthalensis* up into several "races."

The general type is that of a short heavy-boned man. The brain capacity, both sexes considered, varies from about 1,100 to 1,600 cc. The head is long but does not extend very high above the ears. There is a huge supraorbital ridge, a retreating forehead, large eye orbits, a wide and rather prominent (not flat) nose, long upper lip, and little or no chin. The forearm and shin are short in comparison with the arm and thigh, the thumb is opposable, the big toe not (just as in modern man), and there are several apelike characters about the feet. *Neanderthalensis* probably walked more uprightly than many artists have represented.

This hurried survey of man's forerunners has brought us down to the last phase of the Old Stone or early stages of the New Stone Age. Our last representation of preman, *neanderthalensis*, lived during the Old Stone or Paleolithic Age. He had come a long way from Pithecanthropus in physical beauty and probably had progressed mentally as well. So far as is known, he was still a hunter and food gatherer. He had, however, learned to make and use fire, which, together with his earlier toolmaking, was an important step in his emancipation from environmental bondage. No one knows how he lived, but undoubtedly it was a rather precarious existence—killing or catching enough game to piece out the roots, berries, and seeds which he could find, and all the time in danger himself of being devoured. To learn how best to hunt or fish, which foods would nourish and which kill was a long slow process; but, when once learned, it was undoubtedly quickly absorbed into the cultural tradition and passed along to each new generation. Considerable skill, courage, and cooperative effort were undoubtedly needed to hunt the mammoth, bison, wild horse, and reindeer that roamed over the steppes and plains. These hunters undoubtedly followed the herds as they

migrated, north to Russia and Siberia—south to the Danube basin. We get a glimpse of the fauna of the upper Paleolithic through the fact that these peoples carved animals in stone or ivory, drew and painted them on the walls of their caves, and modeled them in clay.

These hunters and food gatherers were content to live on what nature provided though undoubtedly they progressively improved their methods of seizing what nature offered. The first great forward step—that from food gathering to food producing—had to await the arrival of a more ambitious, more intelligent man than *H. neanderthalensis* and the wait was not to be long.

Homo sapiens (Modern Man).—Where *sapiens* came from and when he arrived is not definitely known. We see *neanderthalensis* surviving for perhaps a few thousand years following the last glacial period, say until 25,000 years ago. Then he seems suddenly to have disappeared and to have been replaced by *H. sapiens*. This occurred in the last stages of the Paleolithic, which merged with the Neolithic or New Stone Age, about 10,000 years ago. Speculations regarding the origin of early *sapiens* and his relation to the modern races of man have been numerous; actual data in the case are about negligible. Did he (*i.e.*, *H. sapiens*) come in from Asia or from Africa to blend with or totally supplant *neanderthalensis?* Or did the latter evolve into *sapiens?* All we can do at present is to ask the questions and hope the future may provide an answer.

The "Grimaldi Race."—Near Monaco on the Mediterranean coast in the so-called "Grimaldi caves" there were discovered in 1901 two skeletons, one of a woman, the other of a fourteen-year-old boy. These skeletons are of a distinct type. Both of them were about 5 ft., 2 or 3 in. tall. The leg and arm bones and more particularly the head and facial bones are strongly suggestive of negroid characteristics. They have caused considerable argument in anthropological quarters, but the bulk of opinion now inclines to the belief that they were not representative of a distinct "Grimaldi race" but rather an early and primitive example of a late Paleolithic stock—the Cro-Magnon.

Cro-Magnon Man.—This was the name assigned to five skeletons that were found buried in the Cro-Magnon rock shelter in the Dordogne, France, in 1868. Other finds of this type have been made in various parts of Western Europe. This was probably a fairly tall race, with long heads, a high vertical forehead, short, broad face, prominent nose and chin. The shin and forearm were long in comparison with thigh and upper arm. This type of man, living in the late Paleolithic or Old Stone Age, had a well-developed culture. Certainly they made quantities of flint and bone tools and were excellent artists and sculptors. Their origin is not yet known, and it is believed that they intermingled with

other stocks, and perhaps traces of them are still to be found in men living today. What a fascinating thing it would be if you and I could trace just one line of our pedigree back to the year, say, 13,000 B.C. just to make the wish moderate!

Several other fossil remains of man have been discovered, *viz.*, Wadjak man (Dr. E. Dubois) and Solo man (W. F. F. Opperworth) from Asia; Rhodesian man (A. S. Woodward) and Boskop man (Dr. R. Broom) from Africa. But these, together with several other finds, it has not been possible to place with any degree of satisfaction in the general pedigree of mankind or his collaterals.

In all this length of time, from perhaps 1 million years ago down to 10,000 or 12,000 years ago, man traveled his difficult way without the

FIG. 14.—Neolithic man of the Campignian Stage. Mural painting by Charles R. Knight. (*Courtesy of The American Museum of Natural History.*)

aid of a settled agriculture and animal husbandry. The wonder is of course that he survived at all. He lived side by side with many other mammals, some extant, some extinct. Probably for vast periods of time man has used animals for food and their skins for clothing and shelter. This Paleolithic hunting stage has persisted in some places right down relatively to the present, *e.g.*, in Australia, Africa, and America.

Hunting Stage.—The exact times and places of the domestication of plants are, of course, unknown, and there has been much debate as to whether agriculture preceded or followed the domestication of animals. Opinion at the present leans to the following sequence: first hunting; then a hoe or hand culture, then animal domestication; then agriculture or an animal-power culture; and, finally, the extensive development of herds and flocks into a pastoral culture, although herding may have preceded agriculture in certain areas.

Certainly, we are justified in assuming the hunting stage to have preceded all forms of agriculture or animal husbandry. Man lived at

this time on what roots, berries, and seeds he could find and on such insects, animals, and fish as he could catch. Gradually, we can imagine, he improved his techniques for finding sources of food and utilizing these natural sources so that they would return a better yield. Likewise his techniques of hunting and fishing improved. He learned to trap and spear fish, to make ingenious traps and pits into which animals could be lured or driven, and to disguise himself under the skin or hide of the animal he was hunting in order to permit a closer approach. In this stage it seems safe to assume that the men generally provided the meat portion of the diet, while the women largely supplied the vegetable products. This has led to the assumption that women were probably the real instigators of agriculture.

During this stage of man's development, he had to make the best of his own particular environment. Some regions, no doubt, provided ample game and fish and little food of a vegetable nature, while in some other regions the reverse situation was encountered. Man being omnivorous, this type of enforced adaptation would present no very great difficulties. There were undoubtedly wide variations during this early hunting or food-gathering stage of man's existence. It has sometimes been assumed that these hunters were extensive roamers, but it seems more logical to think of each group confining itself to a relatively small area where they would not come into direct conflict with other groups. Under these conditions, children are a distinct liability, and it seems probable that groups increased at a very slow rate.

Early Plant Culture.—Somewhere man took his first decisive step that was eventually destined to lead him up out of savagery. He had been utilizing such vegetable products as nature had provided him just as he found them. Now, however, he begins to try to control this source of sustenance. He takes wild grasses, wheat, rye, oats, corn, and various bulbs, tubers, and trees and tries in his crude way to control and assist their growth by scratching and preparing the soil, removing weeds, protecting them from animals, and, finally, probably after seeing their more luxuriant growth on dung and refuse heaps, by actually feeding the plants. Thus in many parts of the world and under a great variety of conditions our grains, tubers, and fruits were brought under man's conscious control. Later the creation of one region found its way to a new locality where it sometimes was added to the local accomplishments, and sometimes it totally superseded and displaced the old. This momentous step in man's history occurred after the last glacial period, probably in the early part of the Neolithic.

Closely associated with agriculture was the art of storing and preserving food. Just when it developed is not proved, though man had no doubt been observing similar activities on the part of animals for a

long time. In fact, to have survived at all it seems that man must early have learned how to store up food to tide over periods of shortage. At any rate, after the domestication of plants, there would be more to preserve, and any process that causes man to take forethought is a considerable stimulus to civilization, for it embraces the feature of man's nature which more than any other thing differentiates him from other animal forms. This earliest stage of plant culture (sometimes called "hoe culture") does not imply the use of domestic animals.

The Metal Ages.—The Paleolithic, or Old Stone Age, with its crude stone and bone implements, gradually merged into the Neolithic, or New Stone Age, with its polished stone and bone tools and implements, about 10,000 years ago. Sometime during the Paleolithic Age man learned to use fire, but he had no agriculture and probably no domestic animals except perhaps the dog. Sometime during the Neolithic, agriculture and animal domestication came into being, and these peoples learned how to build shelters of wood.

The ancient stone ages were finally superseded by the various ages of metals. Metals reached Southeastern Europe soon after 3000 B.C. but did not penetrate to Northern and Western Europe until nearly 2000 B.C. The first metals used were copper and its alloy of tin, bronze. This was followed about 1000 B.C. by the Iron Age. Thus the three great ages of stone, bronze, and iron followed and blended into each other, although their dates in different localities may have differed by a thousand years or more, so that Bronze Age here may have been Iron Age there. With the development of better and more durable tools, the improvement of agricultural and animal-husbandry practices, civilization developed new impetus.

Domestication of Animals.—Just when the domestication of animals began is unknown; it certainly was long before there was any thought of, or means for, recording historical data. Domestication very likely began at the end of the Old Stone Age and received decided impetus during the New Stone Age. Each domestic animal has had a rather restricted and humble origin, yet through constant selection for one or another character all of the multifarious forms have evolved—some useful, some ornamental, some having both qualities, and some neither. Selection always has been and always will be the key to animal breeding.

Although the exact beginning of the domestication of animals is unknown, it seems logical to infer that, with the possible exception of the dog, it arose when man ceased to be purely a hunter and adopted a more or less settled mode of living. This new mode of living demanded that food be close at hand. This in turn necessitated plant and animal culture. From that remote time to the present, man has been growing plants and animals, selecting promising variations, and eventually

establishing pure strains of plants and pure breeds of animals. Plants and animals have both reached a stage of marked efficiency through long periods of breeding. Superior animals were no doubt developed by each of the ancient civilizations and suffered retrogression with the decline of the civilization of which such development was a product.

Though its exact time, origin, and mechanism are, and perhaps always will remain, wholly unknown, animal domestication continues to be a lively field for discussion. It is true, also, that if we knew the pedigrees of all our animals back to the very origin of the mammals, we might not be any better fitted to breed good livestock today. Still we like to try to piece the scattered details together into a theory that seems to have some degree of plausibility. Of one thing we can probably be certain, *viz.*, that Neolithic man did not hatch full-blown the idea that animals could help him in his difficult struggle for existence. This is undoubtedly true for the reason that at that time swine did not fatten rapidly, sheep produced no wool, cows gave only enough milk for their calves, and the wild horse was probably quite intractable. True, animals have been of untold benefit to man, but their potentialities have been revealed bit by bit over a period of thousands of years.

All our larger farm animals belong to one order, the ungulates or hoofed animals; cattle, sheep, and goats to one smaller group, Pecora. Why did man select just the animals which he did for domestication? Did he try to domesticate many others and fail? True, when we list all man's domestic animals, we have quite an array—horse, ass, cattle, yak, water buffalo, sheep, goat, swine, camel, llama, elephant, dog, cat, reindeer, guinea pig, rabbit, rat, mouse, poultry, turkey, duck, goose, guinea, silkworm, honeybee—and who knows what other conquests will be made in the future?

For successful domestication, of course, animals had to have the proclivity of breeding in captivity as well as a certain degree of tractability. The dog has had a varied history under domestication. It is thought that he started out as a scavenger living on the outskirts of man's settlements. From this he grew to be a pet, companion, herder and protector, an ally in the chase, a source of food, clothing, and tractive power. No other animal has filled so many human needs as the dog. The reindeer, on the other hand, probably owes his domesticity to his fondness for human urine, which he apparently considers quite a delicacy as a source of salt. Many fowl were apparently domesticated for magic and religious purposes and at the time laid very few eggs. Some tribes domesticated the pigeon just because they liked its looks. In other words, many animals have been domesticated for a variety of reasons, none of which was practical. Even today some native tribes keep vast herds of cattle merely for the pleasure of possession.

On the contrary, travel in the desert without the aid of the camel or in the arctic without the reindeer or dog would have been difficult, if not impossible, as these animals often provide milk as well as transportation and often feed themselves in the bargain. On the contrary, the Egyptians made no use of their hogs and sheep as food, and the Chinese used cattle for thousands of years as beasts of burden but never used their milk.

It seems probable that there were several centers of domestication, but where they were is not known. It is generally accepted that the dog was domesticated, probably from the wolf with whom he will still mate successfully, in the late Paleolithic or early Neolithic. There is no safe or accepted chronological order for the domestication of the larger farm animals. Drawings of cattle, sheep, hogs, and donkeys occur in Egyptian writings dating back to 3000 or 4000 B.C. The horse is mentioned in Babylonian writing about 2300 B.C. and appears in Egypt about 1700 B.C. Camels are mentioned in Mesopotamia in 1100 B.C. How much earlier the actual domestication may have taken place is, of course, unknown.

Influence of Domestication on Civilization.—Many factors have influenced the development of civilization, such as the development of speech and writing, the use of tools, the discovery of fire, and the harnessing of steam and electricity. Along with these we must also place the development of agriculture and the domestication of animals. Certain it is that without agriculture and domestic animals man would of necessity still be a nomad and hunter. The domestication of plants and animals furnished the magic "open sesame" that beckoned man out of his dirty, pinched cave to establish a glorious countryside and later to build great cities. By lifting physical labor from his shoulders, it also freed his mind for the development of science as well as for the contemplation of the beautiful. Domestic animals have long been man's most dependable friends and strongest allies in his task of conquering the world in which he lives. All the energy on this planet originates in the sun and the majority of it is stored here in forms that man cannot use directly, *e.g.*, grass, straw, stalks, etc. Domestic animals are merely machines that man has adapted to convert these stores of otherwise unusable energy into useful forms.

Before he domesticated plants and animals, man was a savage motivated largely by selfishness, with little incentive to provide for the future. Like little children the savage is inclined not to look beyond his immediate interests and pleasures. He lives in the present with little thought for the future. Coming into possession of animals changed this, for their future wants must be foreseen and provided for if they are to be of any real service. Flocks and herds must also have had a

marked tendency to broaden the sympathies of the savage—in short, to lead him out of savagery and start him on his journey toward civilization. Our civilization is greatly indebted to domestic animals, though for the most part we are inclined to take their contribution as a matter of course. There is no instance of any race or tribe of man having reached a high state of civilization without the aid of domestic animals, and the leading and conquering nations have always been far advanced in the arts of husbandry. Domesticated animals have nourished as well as reinforced man's sinews, quickened his mind, and broadened his sympathies, so that it is hardly too much to say that the development of civilization had to wait upon the domestication of animals, even though civilization may always have gotten its start in grasslands or centers of grain culture which could be carried out by unaided human labor.

The Dog.—Available evidence indicates that the dog was the first animal domesticated by man, to be followed next by the even-toed ungulates, or artiodactyls, cattle, sheep, and swine, and, finally, by a representative of the perissodactyls, or odd-toed ungulates, the horse. Besides being first in time the dog still holds first place as man's companion. Cuvier, the great French naturalist, wrote:

> The dog is the most complete, the most remarkable, and the most useful conquest ever made by man. Every species has become our property; each individual is altogether devoted to his master, assumes his manners, knows and defends his goods, and remains attached to him until death; and all this proceeds neither from want nor constraint, but solely from true gratitude and friendship. The swiftness, the strength, and the scent of the dog have created for man a powerful ally against other animals and were, perhaps, necessary to the establishment of society. He is the only animal which has followed man through every region of the earth.

The following portion of a poem by Walter Scott depicting the faithfulness of the dog was inspired by the story of a young man who lost his life by falling from one of the precipices of Mt. Helvellyn. Three months later his remains were discovered at the bottom of a ravine, and his faithful dog, almost a skeleton, still guarding them.

> Darkgreen was the spot: mid the brown mountain heather
> Where the pilgrim of nature lay stretched in decay;
> Like the corpse of an outcast, abandoned to weather,
> Till the mountain winds wasted the tenantless clay;
> Nor yet quite deserted, though lonely extended,
> For, faithful in death, his mute favorite attended,
> The much loved remains of her master defended
> And chased the hill-fox and the raven away.
> How long didst thou think that his silence was slumber?

When the wind waved his garments how oft didst thou start?
How many long days and long weeks didst thou number
Ere he faded before thee, the friend of thy heart?

The dog, an unguiculate, *i.e.*, having claws or nails rather than hoofs (ungulate), belongs to the order of mammals known as the Carnivora, meaning flesh eaters. There are two suborders of the Carnivora, the aquatic carnivores, or Pinnepedia, such as the seals and walruses, and the land carnivores, or Fissipedia, including the dogs, cats, bears, etc.

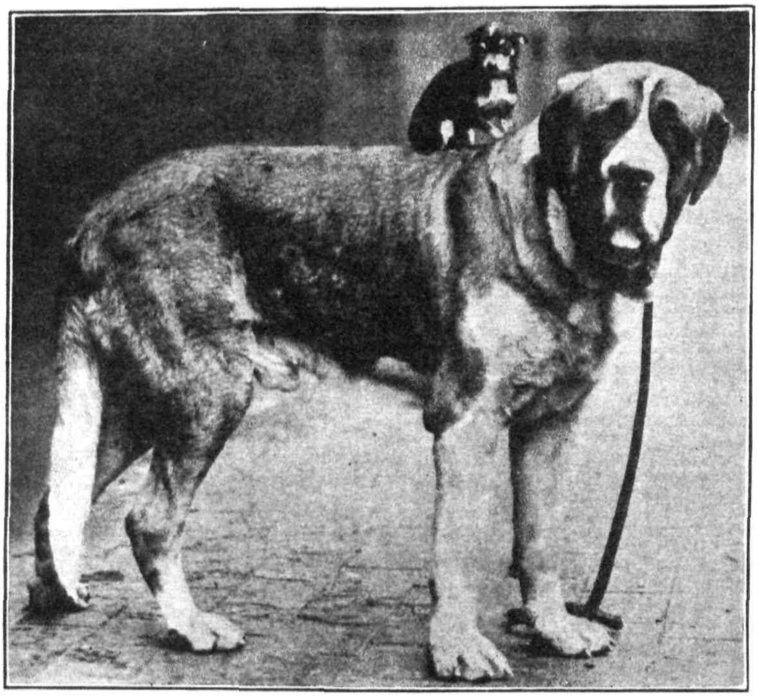


FIG. 15.—St. Bernard (Ch. Blueboy 203 lb.) and Mexican Chihuahua (Rosemary 2 lb.), results of nature's variation and man's selection. (*Underwood and Underwood.*)

The Carnivora have small incisor and large canine teeth with the anterior molars or premolars usually modified for shearing. The Fissipedia include the following families, the Viverridae (genets), Felidae (cats), Hyaenidae (hyenas), Mustelidae (weasels), Procyonidae (raccoons), Ursidae (bears), Protelidae (earth wolves), and the Canidae (dogs, wolves, etc.).

The chief genus of the family Canidae is that called Canis. In this genus are to be found modern domesticated dogs, *Canis familiaris;* as well as the wolves, *C. lupus*, etc.; the jackals, *C. aureus*, etc.; and the foxes, *C. decussatus*, etc. The chief differences between these four species

of Canis lie in the shape of the eye and its pupil. The dog, the wolf, and the jackal are interfertile and their gestation periods are of similar length. The dog has five toes on the front feet and four on the hind feet. The typical dentition in this family is:

Incisors	Canines	Premolars	Molars
$\frac{3}{3}$	$\frac{1}{1}$	$\frac{4}{4}$	$\frac{3}{3}$

Origin and Domestication of the Dog.—The ancient ancestry of the dog is very little known. Owing to the closeness of the anatomical and skeletal features of the dog and the wolf, it is quite generally stated that the dog is an offshoot of the wolf tribe. Possibly savage hunters captured wolf puppies and took them home to amuse the children, and in this way through the course of time the wolf gradually lost his ferocity and aloofness and learned how to bark joyously at his master's approach.

The jackal of the Old World, a smaller, more yellowish wild dog and much less ferocious than the wolf, is believed by some to be the progenitor of the dog. This strain is also much more easily tamed than is the wolf. Some also have suggested that the dog arose as a result of a cross between wolves and jackals. Nothing definite, however, is known regarding the dog's progenitors.

Various breeds of dogs existed during the Roman classical period, and some of these are preserved in sculpture. Dogs are also represented on the Egyptian monuments as far back as 3400 B.C. Skeletal remains of a canine animal are embedded in the Danish middens of the Neolithic, or New Stone Age. The dog has, therefore, been in existence for at least 5,000 to 8,000 years.

The dog may first have served as a source of food for ancient men in times of famine. This in itself would have been a powerful selective agency, as the least valuable would have been the first sacrificed. At a later period, before the time of the advent of agriculture and a more or less settled mode of existence, he no doubt became an invaluable ally in the chase. Later still, certain strains were used for draft as are the Eskimos and other dogs of today. Through it all, the dog has continued to grow in man's affection no doubt because of his sagacity and faithfulness and also because more than any other animal the dog is both capable and desirous of returning any evidence of affection.

There are now recognized six distinct groups of dogs, *viz.*, the greyhound, hound, mastiff, spaniel, terrier, and wolflike. Mason's "Dogs of All Nations" lists 183 breeds of dogs from 39 countries. The variations

in the different breeds of dogs as to size, form, color, degree of harshness and length of coat, skull and jaw shape, length of body and of leg, temperament, vitality, and educability cover a startlingly wide range. All breeds and types of the domestic dog have come, however, from not more than two or three wild progenitors in the comparatively short space of a few thousand years. All of them from the huge St. Bernard to the tiny Mexican Chihuahua are the results of nature's variations plus man's selection.

The Horse.—The name *horse* is equivalent to the Anglo-Saxon *hors*, which means *swiftness*, and it is logical to suppose that this genus was able to survive the vicissitudes of time and enemy attack only because of its speed and mobility.

The only surviving genus of the family Equidae, to which the horse belongs, is that designated as Equus. There are at present four living types: horses, asses, half asses, and zebras. Besides the domesticated horses, *Equus caballus*, there is one wild type found in Mongolia, *E. przhevalski*. The domestic ass is called *E. asinus* and has at least two wild varieties, *africanus* and *somaliensis*. In addition, there are three Asiatic half asses, *E. kiang*, *E. onager*, and *E. hemionus*. Among zebras, which are striped animals, there are three types, *E. zebra*, *E. burchelli*, and *E. grevyi*, and in addition several varieties of *E. quagga* (now extinct). All these species of horses, asses, and zebras are capable of producing hybrids among themselves but the hybrids are, as far as is known, generally sterile.

Equus has two close relatives among the perissodactyls (uneven number of toes), *viz.*, the tapirs and the rhinoceroses. The tapirs are rather heavy, thickset animals with stout limbs having four toes on the forefoot and three toes on the hind foot. The nose and upper lip are elongated into a flexible, mobile snout, the ears small and erect, and the tail short. The dental formula in this genus is $\frac{3}{3}, \frac{1}{1}, \frac{4}{3}, \frac{3}{3}$. The rhinoceroses are very heavy, thickset animals with very short, stout limbs and three completely developed toes on each foot. The head is large with one or two horns on the median line of the face or nose. The ears are erect, eyes small, and the skin very thick and set off into sections of indurated plates. The incisors and canines are generally lacking, giving a dental formula of $\frac{0}{0}, \frac{0}{0}, \frac{4}{3}, \frac{3}{3}$.

The members of the genus Equus are generally taller and swifter animals than their near relatives, the tapirs and rhinoceroses, their greater height being due to a lengthening of the cannon bones and middle toe. The head and tail are also longer, and the body has a much denser hairy covering. There are wide differences in the genus Equus in size,

color, tail, ear, and face characteristics. The dentition of the genus is $\frac{3}{3}, \frac{1}{1}, \frac{3}{3}, \frac{3}{3}$. The horse *E. caballus* is distinguished by a long flowing mane and forelock, smaller head, broader feet, shorter ears, longer limbs, heavier tail, and also by four callosities, one on each limb on the inner surface above the "knees" of the forelimbs and below the hocks of the hind limbs. *E. przhevalski* has a short erect mane. The asses and zebras have narrow hoofs, large ears, chestnuts or callosities on the front limbs only, a short mane, and short hairs on the tail. The wild asses or half asses are intermediate with fairly long ears, a short mane, and only the front feet narrow.

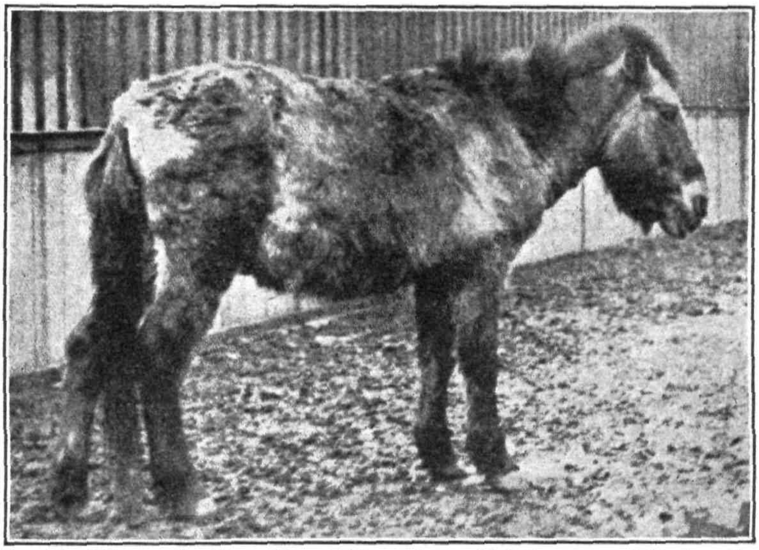
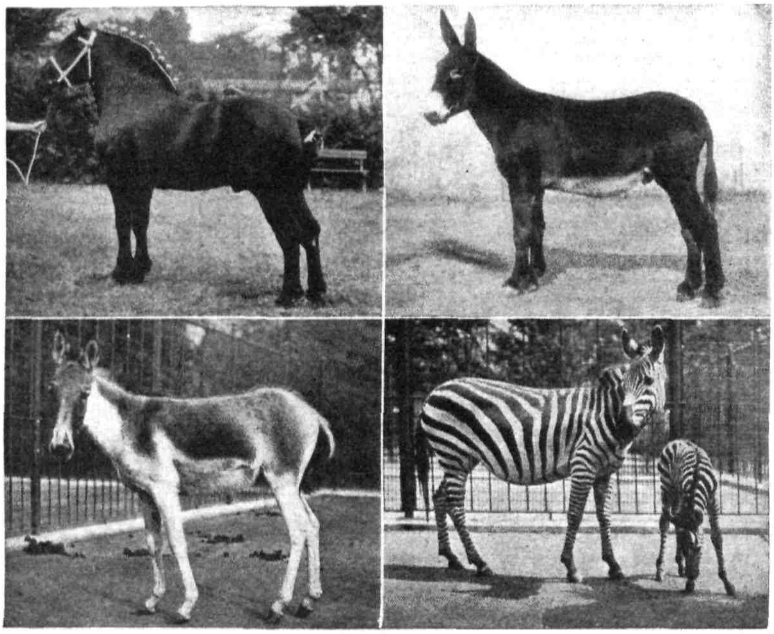


FIG. 16.—The "Tarpan," a Mongolian wild horse from which the horses of Western Europe have been derived. (*From Thompson, Outline of Science, Geo. Newnes, Ltd.*)

Origin and Domestication of the Horse.—The horse was probably the last animal to be domesticated by man, but his immediate ancestry as well as the date of his domestication is still a matter of dispute. It seems probable that at least two or perhaps three wild types have made their contribution to our domestic horse. One of these was no doubt the so-called "steppe horse" now known as the fossil representative of Przhevalski's horse. This was a small, sturdy, short-legged horse with a moderately long, heavy head. Another was the so-called "desert horse," standing as did the steppe horse about 13 hands high and corresponding closely to the now extinct tarpan or Mongolian horse. This strain was somewhat more slender than the steppe horse and had a shorter head. The third contribution was that of the "forest horse,"

a type standing about 15 hands high with longer but stout limbs and having a long, narrow head and long body. It seems probable that all three types made their contribution and that by crossing and selection the foundations of our modern breeds were laid. The horse was apparently domesticated separately in both Asia and Europe, probably earlier in Asia. A Turanian folk tamed the Przhevalski horse around 3000 B.C.

The earliest record of the horse dates back to Paleolithic times about 25,000 years ago. Around an open camp at Solutré in France are found



Horse Ass
Kiang Zebra
FIG. 17.—The horse and some of his close relatives. (*Courtesy New York Zoological Society.*)

the remains of several thousand horses, indicating that they may have served as a source of food. In later Paleolithic times, rock carvings of the horse were made but do not show him harnessed, ridden, or attached to any sort of vehicle, so that we assume the horse was not yet fully domesticated.

The earliest trace of the horse hitched to a chariot goes back to about 2000 B.C. in Greece, whereas the first Egyptian records of the horse date from about 1600 B.C. These were small horses about 13 hands high, similar to Przhevalski's horse. The horse evidently grew in size and importance in Persia and Mesopotamia during the intervening years and after about 750 B.C. began to serve as a mount. Mounted horsemen

were first given a place in the Olympic games in 648 B.C. The Arabs did not use horses until after the time of Christ.

The development of the Arabian horse by the Bedouins of the desert is generally recognized as the first great achievement in animal breeding of which there is any definite record. Because the Bedouin's safety often hinged upon the speed and endurance of their horses, these people surrounded their breeding operations with an air of superstition and mystery, much of which has persisted in certain quarters to the present day. The Arabian breed probably was used later to refine the large "cold-blooded" horses of the countries to the west and north, particularly of France and England. The Arabs, as well as Barb and Turk horses, were also used to cross with the racehorse of England, thus laying the foundation for the Thoroughbred.

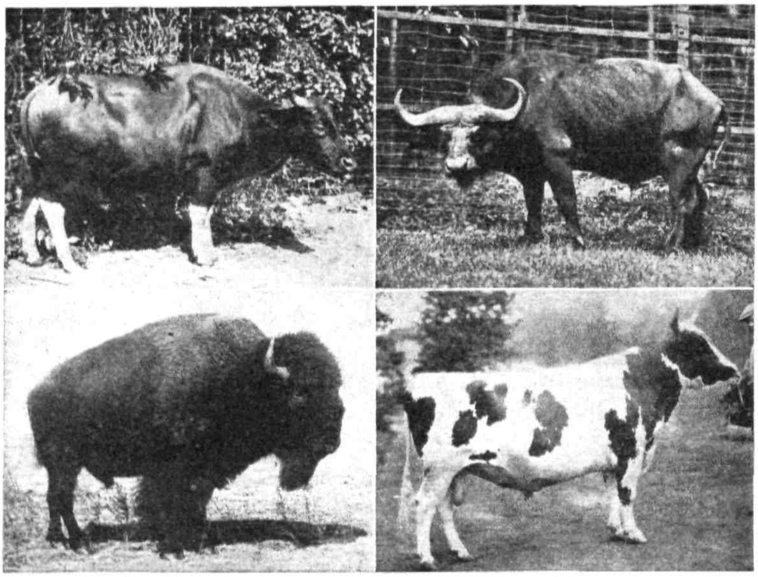
For many centuries the horse has been man's foremost helpmate in work, war, and play. He rendered incalculable assistance in conquering the New World, America. From 4,336,000 horses in 1840, the year of the first agricultural census in the United States, his numbers steadily increased to 21,500,000 in 1918. Since then he has been replaced to a considerable degree by machines, automobiles, trucks, and tractors, so that in 1940 his numbers had dwindled to about 10,000,000. This freeing of land from the production of feed for horses has complicated the situation of agriculture tremendously, and there seems now to be a definite movement toward the restocking of our farms with horses. What the future holds in regard to mechanization no one can prophesy, but it can be said with little fear of successful contradiction that our present civilization rests quite largely on the sturdy legs and broad backs of our four-footed friends and not the least among these is *E. caballus*.

Cattle.—The Pecora, or true ruminants, is made up of the following families: the Cervidae (deer), Giraffidae (giraffes), Bovidae, to which all types of cattle belong, as well as sheep, goats, and true antelopes. Both sexes in this family are usually horned. The horns are hollow and grown on bony cores and arise from the frontal bones. The second and fifth digits are rudimentary or absent, the third and fourth fully developed. The dental formula for this family is $\frac{0}{3}, \frac{0}{1}, \frac{3}{3}, \frac{3}{3}$. These animals are ungulates or hoofed and belong to the group known as artiodactyls, or even-toed. There are one or more enlargements for food storage along the esophagus, usually three, and the members of this family ruminate or chew their cuds.

The genus Bos includes the taurine group, *Bos taurus* (cattle); and *B. indicus* (humped cattle); the bibovine group, *B. gaurus* (the gaur); *B. frontalis* (the gayal); and *B. sondaicus* (the banteng); the bisontine

group, *B. grunniens* (the yak); *B. bonasus* (the European bison); and *B. bison* (The American bison); the bubaline group, *B. caffer* (the African buffalo); *B. bubalis* (the Indian buffalo); *B. mindorensis* (the Mindoro buffalo); and *B. depressicornis* (the Celebes buffalo). There are many varieties under most of these species, both living and extinct. As far as known, all these species are generally interfertile and produce fertile hybrids, though the males are often sterile.

These close relatives of our modern domesticated breeds of cattle form a very interesting and widespread group of mammals. Many



Gayal — African Cape Buffalo
American Bison — Ayrshire Bull
FIG. 18.—Some close relatives in the genus Bos. (*Courtesy New York Zoological Society.*)

of them have become domesticated. Of the Bibovine group, the gaur (*B. gaurus*) is the largest of the present-day representatives and is found in India, Burma, and all the Malayan regions. It has somewhat flattened horns, a short tail, white lower extremities, or "stockings," fine silky hair, and long spines on the anterior thoracic vertebrae forming a high set of withers, the bull standing about 16 hands high. It is a somewhat shy, forest- and hill-loving animal. The gayal is somewhat smaller with short horns and "stockinged" feet and is easily domesticated. The banteng is the smallest representative of this group, has a white disk from the hocks to the tail setting, and is somewhat longer legged. The banteng frequents the lowlands as well as the hills.

The bisontine group includes the yak of Tibet as well as the European and American bison, the latter often erroneously called a buffalo. The yak inhabits the wild, cold regions of Tibet and Siberia, and it is said that travel there without his help as a pack animal would be impossible. The yak has a skirt of long hair hanging from his shoulders, flank, thighs, and tail. He is smaller than the gaur, standing about 14 hands high, and is not "stockinged" with white. The bison is characterized by very heavy forequarters and light rear quarters. His head, neck, chest, and shoulders are covered with moderately long, dark hair and like the yak he has 14 or 15 pairs of ribs. Great herds of bison once ranged over most of Europe and a goodly portion of North America.

The bubaline group, or true buffalo, includes four species at present. The African buffalo is noted for his very heavy downcurving horns, which almost meet in the mid-line of his face, very unlike the Indian buffalo with his wide, out- and upcurving horns. The Indian buffalo is also larger, standing 15 to 16 hands high. Both the Philippine and Celebes buffaloes are much smaller in stature, and in the latter the horns grow straight back and upward from the forehead resembling the horns of an antelope. The buffalo is generally found in low, swampy regions.

Origin and Domestication of Cattle.—It seems probable that cattle were domesticated during the New Stone Age in Europe and Asia from more than one wild form. There are two types of domestic cattle now living, *B. indicus*, the humped cattle of tropical countries, and *B. taurus*, of the more temperate zones. Humped cattle were domesticated as early as 2100 B.C. Cattle play an important part in Greek mythology, were sacred animals in many older civilizations, and their slaughter was therefore forbidden. The great ox or aurochs, *B. primigenius*, which Caesar mentioned in his writings, is generally considered to be one of the progenitors of our modern-day breeds. This was a very large animal and described by Caesar as "approaching the elephant in size but presenting the figure of a bull." The wild park cattle of Britain are considered by some to be the direct descendants of *B. primigenius*. Another progenitor of our modern breeds is *B. longifrons*, a smaller type, with somewhat dished face. This is the Celtic Shorthorn which has never been found except in a state of domestication and was the only ox in the British Isles until 500, when the Anglo-Saxons came bringing with them the great ox or aurochs of Europe.

It is doubtful whether any of our present-day European or American breeds trace solely to either one of these ancient types. It seems much more probable that our present breeds are the results of various degrees of crossing between them. The cattle of India and Africa, *B. indicus*, are characterized by a lump of fleshy tissue over the withers sometimes

weighing as much as 40 or 50 lb. They also have a very large dewlap and the voice is more of a grunt than a low. They are thought to be descended from the wild Malayan banteng.

It seems probable that savage man first used members of the family Bovidae as a source of food. Real domestication began when these animals were used as draft animals, probably in the first faltering steps of the beginning of agriculture or the tillage of the soil. In their wild state there was little tendency to store excess fat on the body, as this would have been a hindrance rather than a help under the conditions then existing. Milking qualities also were just sufficient for the rearing of the young. As civilization developed, feed became more abundant, methods of caring for livestock improved, and the latent possibilities for rapid growth, fat storage, and milk production began to be realized under man's selection.

That the ox played an important part in man's aesthetic development is attested by its use in architecture and interior mural decoration as well as its frequent use as a subject of poetic fancy. The ox assumed great religious importance in many ancient civilizations, and the best members of the breed were sacrificed to propitiate the gods. They were crowned with wreaths and honored in other ways during the pageants and holidays, and to some extent we perpetuate this custom in our fairs and expositions today. The Romans used the term *pecunia* for money, a word derived from *pecus* meaning cattle, and in ancient times a man's wealth was figured in terms of his cattle possessions.

Down through the ages various members of the genus Bos have continued to be one of man's most useful allies. Without their contribution of power, meat, milk, and inspiration it is difficult to visualize the possibility of an advancing civilization. The following is G. L. Bickersteth's translation of Carducci's poem, "The Ox."

I love thee, holy ox; a soothing sense
Of power and peace thou lodgest in my heart.
How solemn, like a monument, thou art,
Watching the pastures fertile and immense!

Or 'neath the yoke with calmness how intense
Dost thou to man's quick toil thy aid impart!
He shouts and goads thee; patient of the smart,
Thine eyes, slow turning, claim more reverence.

From thy broad nostrils, black and moist, doth rise
Thy breath in fragrant incense; like a psalm
Swells on the air thy lowings' joyful strain.

Austerely sweet are thy grave emerald eyes,
And in their depths is mirrored, wide and calm,
All the divine green silence of the plain.

Sheep and Goats.—These two genera of the family Bovidae are very closely related, so closely in fact that a naturalist never speaks lightly of separating the sheep from the goats. Modern breeds are easily enough distinguishable, but the task is sometimes very difficult in their wild relatives. The genus Ovis includes the sheep and its wild relatives, whereas goats and their kind make up the genus Capra. Sheep are to be distinguished from goats by glands in both fore feet and hind feet, by the absence of a true beard, and by the absence of the strong goaty odor in males. There are also marked differences in the skulls, and the horns generally spiral in opposite directions, the right horn of the sheep to the right like a corkscrew, and the goats to the left. The sheep gets its Latin name *Ovis* from the Sanskrit *avi*, signifying to keep or to guard. It is said that some at least of the domesticated breeds of sheep and goats are interfertile and produce fertile hybrids.

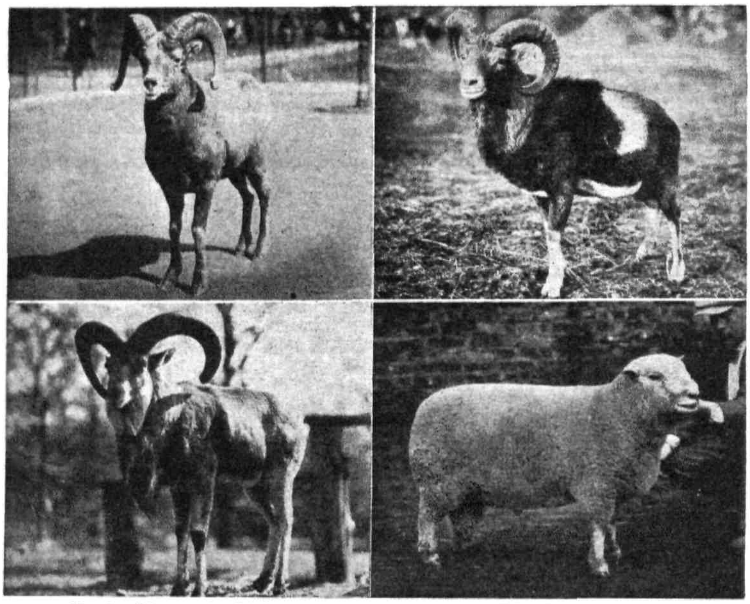
Our domestic sheep have a great variety of wild relatives. Lydekker divides these into four groups: (1) the bighorn (*Ovis canadensis*) of North America and Kamchatka, (2) the argali (*O. poli*) of Central Asia, (3) the urial (*O. vignei*) of Asia and the mouflon (*O. musimon*) of Asia Minor and Europe, and (4) the bharal (*O. nahura*) of Little Tibet and the Barbary (*O. tragelaphus*) of North Africa.

The bighorns are a large breed of wild sheep standing 38 to 42 in. at the withers. As the name indicates, the horns are very large and are noted for the small size of the transverse ridges and the prominence of the outer anterior angle of the horn. The horns curve back, out, down, and forward in a bold sweep. The upper part of the body is covered with dark hair, the lower portion with a gray or dirty white hair. They have a very noticeable caudal disk of light-colored hair extending in a radius of about 8½ in. from the root of the short tail. They make a square track, for the interior and exterior edges of the toes are nearly parallel. The front of the toe is also beveled, which accounts for the remarkable climbing power of this group of mountain-dwelling wild sheep. The group has a very shallow lachrymal pit in the skull.

The argali, or Marco Polo's sheep, is a large species standing 40 to 48 in. high at the withers. They have strongly marked transverse ridges on the horns and a less pronounced outer anterior angle. The horns are very long (circle and a quarter) and make a wide sweep. The color of this group is very similar to that of the bighorn, including the caudal disk. These, however, have a short mane on the throat. These wild sheep inhabit the grassy slopes of The Pamirs and never attain to

very high altitudes. There are several closely related varieties in this group differing somewhat in size, color and shape of horns, habitat, etc.

The urials are a smaller race of sheep generally found in high altitudes. They stand about 3 ft. high and have shorter horns than the bighorns or the argalis. The general color is brownish gray with a white belly. The throat has a short beard or mane. There are several differing varieties in this group also, including the mouflon of Sardinia and Corsica. This is a small species of brownish-gray color with lighter colored underline and legs.



Rocky Mountain Bighorn — Mouflon
Punjab — Southdown
FIG. 19.—The sheep and some of its cousins. (*Courtesy New York Zoological Society.*)

The bharal in many ways stands intermediate between sheep and goats. Its horns lack the deep transverse ridges of the sheep and are a dark olive-green color like the goats. It has a longer, therefore more goatlike tail, and it lacks the lachrymal gland on the face. On the other hand, it lacks the strong odor of goats, also lacks a beard, and like the sheep has glands between the toes of all four feet. The bharal stands about 30 to 36 in. high and is a dark slaty blue color. There is no long hair on the throat or tail. The skull characteristics of the bharal are goatlike rather than sheeplike.

The wild relatives of the goat include the ture, the pasang, generally regarded as the true progenitor of all our modern domesticated breeds

of goats, the ibex, the markhor, and the tahr. Here again we find a very wide variation in superficial characteristics among the mountain-dwelling members of the genus Capra, a detailed description of which cannot be entered into here.

Origin and Domestication of Sheep.—The sheep probably originated in Europe and the cooler regions of Asia not further back than the Pleistocene or later Pliocene. Remains of a sheep or goatlike animal have been found at the sites of the Swiss lake dwellings of Neolithic times. Sheep are thought to have been derived from the antelopelike animals allied to the gazelles because of certain similarities of the molar teeth. It seems certain that our modern breeds trace back to at least

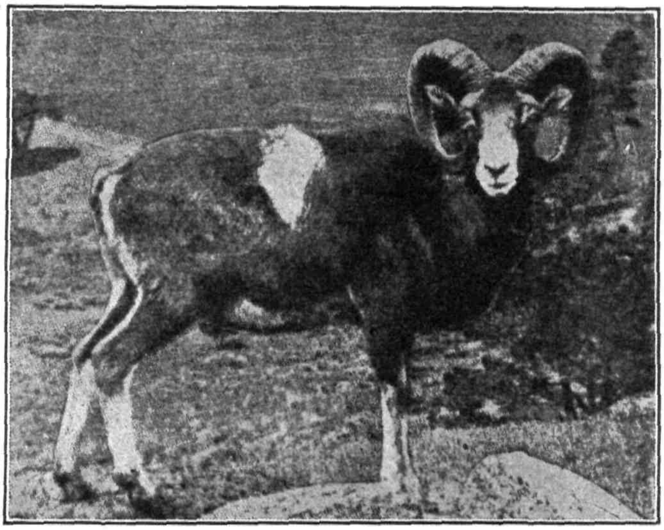


FIG. 20.—The Mouflon—a wild sheep lacking uniform color and having an exterior coat of hair. (*From Coffey, Productive Sheep Husbandry, J. B. Lippincott Company.*)

two remote ancestors, the mouflon of Europe (*O. musimon*) and the Asiatic urial (*O. vignei*).

The sheep, most important of wool-bearing animals, was originally, as in the case of some breeds still, a hairy animal with an underfur of wool. No doubt people living in cold climates who used skins as clothing were the first to begin the selection of sheep for wool production. As in all our domesticated animals, there is wide variation among sheep. Some, like the African long-legged and Abyssinian maned sheep, bear hair instead of wool, some have spiral horns 2 ft. or more in length, others no horns at all. The tail of the common, domesticated sheep is long and slender; in some other strains, it is loaded with fat and is 1 ft. in width, whereas still others have merely a vestige of a tail. The last

sort often carry hugh patches of fat on the rear quarters, the stored fat in all cases serving to tide the animal over periods of food shortage. The hunia, a tall, long-legged sheep, is used in India as a fighting animal, being pitted against its fellows or other animals.

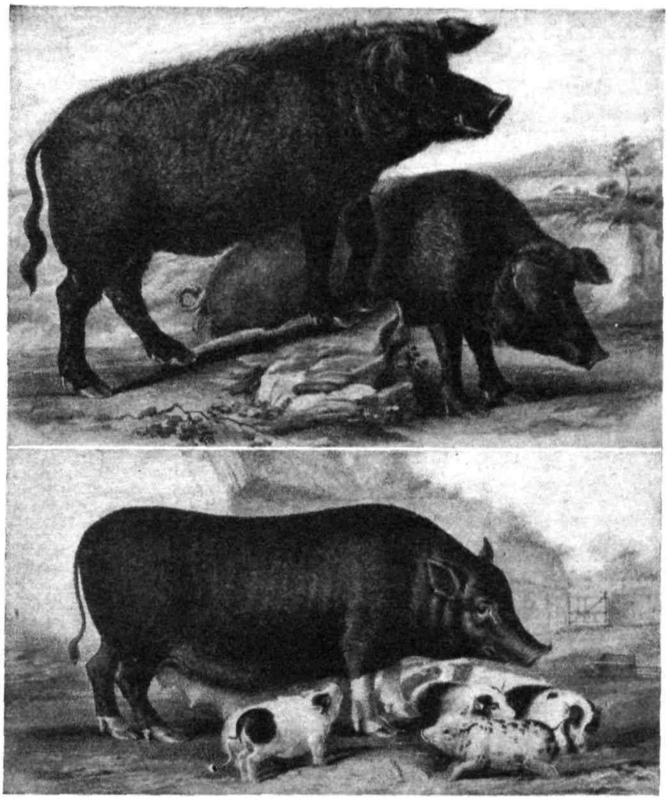
Goats are also versatile in characteristics, yielding the underfur, for Cashmere shawls, and mohair, milk, meat, and draft power and also providing one means of clearing up brush land because of their fondness for all sorts of tender shoots.

Swine.—Swine are ungulates belonging to the suborder artiodactyls (even-toed). They belong to the family Suidae. The Dicotylidae, or peccaries, and the Hippopotamidae, or hippopotamuses, are closely related families, these three families comprising the Suina. These animals have tubercles on the molar teeth, and in them there is not found a complete fusion of the third and fourth metapodials to form a "cannon bone." The nose is elongated into a more or less mobile snout. The typical dental formula for this group is $\frac{3}{3}, \frac{1}{1}, \frac{4}{4}, \frac{3}{3}$, though this is not complete in all forms.

The genus Sus includes, besides the domesticated pig, several wild species. Among them are *Sus scrofa*, the European wild boar; *S. cristatus*, the Indian wild boar; *S. andamanensis* of the Andaman Islands; *S. salvanius*, from the foot of The Himalayas; *S. vittatus*, *S. verrucosus*, and *S. barbatus* of the Malayan region; *S. africanus* and *S. procus* of Africa. The foregoing species vary greatly in size, color, length of coat, length of tail, presence or absence of crest on the neck, size of tusks, number of mammae, etc. The Indian wild boar stands 30 to 40 in. high, whereas *S. salvanius* measures only 11 in. over the shoulder. The tusks of the wild boar are several inches long, those of the red river hog, *S. africanus*, only as long as those of the domestic boar, and those of *S. salvanius* are very short. The young of all the above-mentioned species are born with longitudinal dark stripes on the body which disappear as the animal matures.

Other wild relatives of the pig include the genus Babirussa of Celebes and Burma as well as the genus Phacochaerus. In the former genus the upper tusks of the male do not have their summits abraded by wearing against the sides of the lower ones as in the genus Sus, but instead the upper tusks arise close to each side of the face and pass right out through the top of the nose, never entering the mouth cavity, thence sweeping backward and upward, frequently touching the forehead, after which they curve forward, thus resembling horns rather than teeth. These tusks differ from those of the wild boar in not having a covering of enamel. They often measure 14 in. or more in length. These animals are rather "leggy" and almost devoid of hair.

The genus Phacochaerus, or wart hogs, of Africa have a head very large in proportion to the body with eyes placed far back on the face. They derive their name from the wartlike cutaneous lobes that project from each side of the face. Their upper canines are even more greatly developed than those of the Babirussa, curving upward and inward and being large disproportionately to the size of the skull. In older animals all the teeth except the four tusks and the four last molars disappear.



Wild Boar and Sow
Siamese Sow and Pigs
FIG. 21.—Probable progenitors of modern swine. (*Courtesy Longmans, Green & Co.*)

The molars, however, measure more than 2 in. in length from front to rear, the lessened number of teeth being compensated by the over-development of those remaining, which assures ample grinding surface. This development also occurs in the case of the adult elephant, except that in this species the lower tusks are also wanting. Wild pigs are found only in the Old World, their place in America being taken by the peccaries, a distinct family.

Origin and Domestication of Swine.—It appears that our modern breeds, *S. domesticus*, have descended from at least two wild stocks; the Northern European breeds from the wild boar *S. scrofa*, and those of Southern Europe, Asia, and Africa from one of the Malayan pigs, possibly the collared pig *S. vittatus*. The former was a larger, coarser animal throughout than the latter and had a denser covering of hair.

Present-day breeds are no doubt the result of varying degrees of crossing between the parent stocks and their offspring. It seems probable that the pig was domesticated later than cattle and sheep and previous to the horse. Selected for his ability to fatten rapidly and economically, the pig is foremost in converting feed into flesh and second to none in the economy of American meat production. Most of the breeds of hogs found in America are of our own breeders' making; *e.g.*, the Duroc-Jersey, the Poland China, and the Chester White breeds are strictly American creations.

In addition our breeders have developed the American Saddle Horse, the Standardbred horse, the Morgan horse, and a few breeds of sheep. For the most part, however, the American breeder's task has been simply to improve foreign breeds and to render them more suitable to our conditions.

Summary.—We have tried in this chapter to outline the events leading up to the appearance of *Homo sapiens* on this planet. He came upon the scene by slow and probably painful stages. Finally, some 10,000 to 25,000 years ago, he emerged, and his progress has been quickening ever since. We surveyed his early hunting, plant-culture, and, finally, animal-domestication phases and attempted to trace the origins of his four-footed servants. Each successive stage encouraged and made possible a larger human family. By the year 1800, man numbered 750,000,000. Then came the agricultural and industrial revolutions. Food became relatively plentiful, and man's procreative powers responded so well that during the next 140 years population on the earth trebled, reaching a total of over 2 billion. The world has been filling up, perhaps too fast. There are no longer frontiers but in some parts of the world we have caught a glimpse of the abundance that should be the reward of every man of intelligence and energy. Science has now placed in our hands the tools for producing abundance. We have yet to decide what to do with them.

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CHAPTER III

ANIMAL ORIGINS AND PROGRESSION

Animals are organisms that are capable of sensation and voluntary movement. Some are one-celled, others many-celled; some move in the air, some on land, some under water; some have their supporting structures, if any, on the outside like an overcoat and are called *invertebrates;* some are supported by a bony or cartilaginous inner framework and are called *vertebrates*, species of the former far outnumbering those of the latter. Some, like man, have a very highly developed brain and sensory system for recording environmental stimuli; others, like the clam, are relatively immune to environmental changes. All must ingest food materials and oxygen and rid themselves of waste products in order to live. All are endowed with the power and "desire" to perpetuate their kind through some form of reproduction. Although they show the widest sort of diversity, there seems to be a thread of unity binding all living creatures into one organic whole. They all come into being, grow to maturity, reproduce their like, and, finally, die in very much the same fashion.

Early Ideas on the Genesis of Living Forms.—Man has been pondering the question of the whence, why, and whither of himself and all other animate nature for many thousands of years. These questions probably did not concern him in his prehuman state, any more than they concerned you and me when we were infants. With the dawn of reason and beginning of the capacity for reflective thinking, however, man began to wonder about the origin of and relationship among living forms. Until the advent of science with its inductive method of reasoning, he could but guess and speculate on these questions.

Science is nothing but the discovery and arrangement of separate facts into logical patterns of relationships or of cause and effect, the ascertaining of general laws from separate facts. Millions of facts, classified into many categories, indicate relationship between all living forms. For a full appreciation of the problems of breeding and inheritance, an understanding of the general scope of animal relationships furnishes the best medium.

Centuries ago it was obvious that the sun revolved around the earth, men saw it happen every day. It was just as obvious that the earth was flat. In this same category of the obvious was the production

of living matter from lifeless materials; maggots and flies from decaying meat, worms from manure, etc. This idea of spontaneous generation of living organisms from dead material is, therefore, of ancient origin and is probably still extant in some regions.

Most of the early Greek philosophers felt the need of offering some explanation of the genesis of living forms. Thales (seventh and sixth century B.C.) was the originator of the doctrine of abiogenesis, or the production of living forms from lifeless matter. He taught that life develops from amorphous slime under the influence of heat. Anaximander (611–547 B.C.) taught that the earth existed first in a fluid state, which later solidified in spots to form dry land, and that living creatures formed in the water came out onto the land in a gradual fashion and acquired the appendages and other bodily mechanisms which would make terrestrial life possible.

Anaxagoras (510–428 B.C.) was the first to suggest the idea that gradual development was not the result of the workings of blind force but was directed by some "Intelligence," a theory known today as *teleology*. His idea was that the germs of all animate and inanimate things existed first in chaos, but that gradually soil was laid down, covered with air, and this in turn by ether. The germs of plants floating in the air finally settled on the earth and covered the earth with vegetation. Thereupon the germs of animals and men, which he supposed were floating in the ether, settled onto the earth, grew, and prospered. All of this, according to Anaxagoras, followed an intelligent plan created by some designer; *i.e.*, the process was not inherent in the materials but needed an outside directing force.

Empedocles (500?–430? B.C.) had the notion that parts of organisms, heads, arms, legs, etc., existing first in separate states, were finally brought together into whole organisms through the triumph of love over hate, and that those which had made a lucky combination of suitably adjusted parts were able to survive and perpetuate themselves in their offspring, leaving others, less fortunate in their acquisitions, to extinction. Here we meet for the first time the general idea of the survival of the fittest.

Epicurus (341–270 B.C.) and his later Roman apostle Lucretius (99–55 B.C.) taught that plants and animals arose on the earth from the action of the sun's heat on the moist earth, or, as Lucretius phrased it in his materialistic poem "On the Nature of Things," "Nothing from nothing ever yet was born." Lucretius anticipated Dalton and modern chemistry in his reference to the atomic nature of matter as well as Mendel and modern genetics in his reference to hereditary bodies within the mother.

Aristotle (384–322 B.C.), one of the most renowned of the Greek philosophers, believed, as did Anaxagoras before him, that some intelli-

gence, entelechy, or "soul of living things" directed the process of the active generation of living forms from passive matter. This soul property was thought to be present in increasing degrees in earth, water, air, and fire, so that the earth produced plants, water produced aquatic animals, air gave rise to terrestrial organisms, and fire the supposed inhabitants of celestial bodies. Aristotle maintained that plants and many animals, *e.g.*, worms, insects, crabs, and other marine forms and even man, might arise spontaneously, all the former from the dew, slime, manure, sweat, meat, decaying trees and fruit or seaweed, or from the moist earth, whereas man's first appearance was thought to have been in the form of a worm. Aristotle's teachings dominated men's thinking down to the time of science, and the acceptance of his ideas by St. Augustine (A.D. 354–430) established spontaneous generation as a dogma of the Church. St. Augustine and others of the early Church fathers, however, were not literalists in regard to the Mosaic account of creation but interpreted the 6 days of creation to be periods of time much in excess of 24 hours.

Aristotle's works were translated by the Arabs in the ninth century and found their way into Spain a century later. The revival of these pagan Greek ideas caused considerable friction in the Western European Christian world of the twelfth and thirteenth centuries, but a synthesis of Greek scientific and Christian theological ideas was finally achieved by the great churchman St. Thomas Aquinas (1215–1274).

Unlike Aristotle, who wanted to understand and eventually control nature for beneficial human ends, the churchmen of the Middle Ages started with some acceptable belief. Their ideal was the contemplation of truth arrived at through intuition and faith. They believed that they knew the purpose and meaning of existence and that the function of nature and of man was to glorify God. The Scholasticism of St. Thomas was a synthesis of Greek reason and Christian faith on the theory that reason and faith are not antithetical but supplementary, and that faith can go beyond reason and solve problems for which reason is inadequate. Intuition was thus judged to be superior to reason, and for 600 years this idea, together with the authoritarianism founded on Aristotle's works, prevented scientific inquiry into the nature of the universe and man. All inquiry into the nature of things thus became heresy, and for nearly 600 years anyone who deviated from this pattern was forced to recant.

But the flame of curiosity was not entirely extinguished, and the noted Italian Leonardo da Vinci of the fifteenth century, scientist as well as painter, pioneered in the field of paleontology, one of the pillars on which the theory of the gradual diversification of living forms now rests. In the sixteenth century, Giordano Bruno (1548–1600) espoused the Greek idea of gradual development and left among other maxims, "The investi-

gation of Nature in the unbiased light of reason is our only guide to truth." He was finally burned at the stake for his refusal to recant his heretical beliefs.

From the liberal ideas of the early Church fathers, the pendulum swung, by the middle of the sixteenth century, clear over to the extreme literal position. Separate creation and the general over-all authority of the Bible both as spiritual guide and scientific textbook were firmly entrenched, and all doubters or too persistent seekers of nature's truths by means of reason or experiment were labeled heretics and forced to recant or be liquidated.

In the last half of the sixteenth century, and still more in the seventeenth century, curiosity and experimentation began to make some headway, but spontaneous generation held its place in the minds of men like Harvey (1578–1657), Descartes (1596–1650), Newton (1643–1727), Buffon (1707–1788), and even Lamarck (1744–1829).

Redi (1626–1697) was the first to show that decaying meat or fish could not produce maggots if flies were prevented from laying their eggs thereon. Leeuwenhoek (1632–1723), the Dutch naturalist, revealed, through his invention of the microscope, a whole new world of tiny living forms, which tended to strengthen the belief in spontaneous generation although he himself considered the forms of organisms infesting rotting meat, etc., to be air-born. Spallanzani (1729–1799), the Italian scientist, Schwann (1810–1881), the German anatomist, and many others devised experiments to try to disprove spontaneous generation in materials uncontaminated by organisms and were generally, though not always, successful. It remained for Louis Pasteur (1822–1895), the great French chemist, to provide, by means of his bent-necked flasks, the final obituary to this age-old idea of spontaneous generation of living organisms.

There are three possible ways for accounting for life on the planet Earth. Spontaneous generation in its ancient sense seems to have been finally ruled out. To think that life was wafted to this planet from some other heavenly body only moves the problem back one step where it is entirely insoluble, and modern astronomical conceptions lend no support to the plausibility of the idea. Still a third possibility is to say that life has existed and will exist eternally. This again is impossible of proof and not very satisfactory to a practical mind.

Modern Ideas of the Beginning of Life.—From Pasteur's work came the final proof that fully formed living organisms cannot be formed in an instant and *de novo* in any sort of a culture. By some this was interpreted to mean that there could never be or have been a transition from nonliving to living material. We know, however, that dead bodies of animals and plants are finally broken down into inorganic compounds or into the elements. The question is whether the reverse process could ever have

taken place. It is now coming to be generally agreed that it not only could but did so happen, not that we now have final proof or that the biochemist can now make life.

The most probable general steps in the process seem to be about as follows: (1) the pulling out of material from our sun by the near passage of another star some 1 or 2 billion years ago and the centralization of this material to form our planetary system, including the earth with its central molten metal core covered by a layer of igneous rocks and enveloped in an atmosphere of aqueous vapor; (2) formation of hydrocarbons by the interaction of carbides of iron and other metals and water; (3) formation of ammonia by the interaction of metal nitrides and water; (4) production of numerous high-molecular compounds through condensation, polymerization, and oxidation-reduction reactions of the derivatives (alcohols, aldehydes, ketones, organic acids, etc.) of the primitive hydrocarbons and nitrogen-bearing compounds to form simple compounds of a protein nature; (5) formation of a primary colloidal system; (6) natural selection of those colloidal systems with a highly developed physico-chemical organization surrounded by a semipermeable membrane capable of reproducing themselves and also capable of continued growth and variation.

This is admittedly a very sketchy picture. Detailed knowledge of the internal structure of the simplest living forms is not now available. Nature has been made to yield many of her secrets, and it seems not improbable that the true nature of living matter will sometime be discovered. Granted the formation of even the simplest living and reproducing forms together with the principle of variation, an orderly progression of living forms from the simplest to the most complex becomes thinkable.

One-celled to Simpler Living Forms.—Students as well as laymen are sometimes prone to look upon single-celled organisms as the smallest and simplest manifestation of life, but this is an erroneous view. The single-celled plant or animal is actually very complex and endowed with the capabilities of nourishing itself, of getting rid of its waste products, and of reproducing. The planet Earth is thought to have existed for about 2 billion years, and it seems probable that, after life arose from inorganic materials, it took several hundred million years to work up to the level of single-celled plants or animals.

Let us then start with single-celled forms but reverse the usual process and try to work back to the original form of life, though we should be wary and not expect to get a necessarily definite answer at the present. The single-celled organism, *e.g.*, amoeba, yeast, etc., as already indicated, is a complex structure and is organized in a definite way. It consists of a cell wall surrounding cytoplasm in which are located chloroplasts, chromoplasts, leucoplasts, chondriosomes, centrosome, fat droplets,

mineral deposits, yolk granules, and a nucleus, the latter often containing dark-staining bodies called *chromosomes*. It has now been established that the chromosomes are the bearers of hereditary potentialities in the higher plants and animals and, therefore, form the bridge of inheritance between succeeding generations. The chromosomes are aggregates of genes arranged in linear series, whereas the genes themselves are probably complex organic molecules.

As we start down the scale in size, we come first to the bacteria. There are many thousands of these forms and in general they are rod-like, round, or spiral-shaped. We are inclined to think of them as enemies to man as those which cause typhoid, pneumonia, and other diseases surely are, but there are thousands of them that are harmless to man and many more which are definitely beneficial, *e.g.*, those soil bacteria which fix nitrogen from the air, those which convert alcohol to acetic acid, or milk curd to cheese.

Ordinary bacteria range in size from about 500 to 750 mμ. Even the highest powers of the microscope cannot at present disclose much concerning their internal structure, although we have a right to believe that they do have a very definite and specific structure. They produce variations that are definitely heritable, and, although we are unable to see a nucleus and its chromosomes within them, it seems a fair assumption that they do actually have some such mechanisms. Stoughton (1929) and Barnard (1930) have shown that at the time of fission the scattered chromidia of certain bacteria aggregate into an ill-defined mass within the organism, which then divides to produce two cells. Here apparently the genetic or hereditary materials are scattered, whereas in the one-celled organisms, discussed above, they have become definitely and permanently organized into chromosomes.

It is known that living entities of a diameter below 300 or 400 mμ exist, although they cannot be seen even with the most powerful microscope we now have. These materials are called *filtrable viruses* or *filter passers* and are the cause of certain diseases such as smallpox, yellow fever, rabies in man, and foot and mouth disease in cattle and swine; but, as with the bacteria, there may also be beneficial ones. Some of them have been photographed in recent years by means of the shorter wave ultraviolet light and more recently with the electron microscope. Although they cannot be seen, they undoubtedly are living materials, for they can produce their like on suitable culture media. In size the viruses are thought to scale down to about 10 mμ.

In the same range of size are also found the bacteriophages, or bacterium eaters. These agents live on young cultures of bacteria which they cause to disintegrate or dissolve. As the amount of bacteria decreases, the amount of phage increases. As the viruses can live only

on living culture tissue so can the various phages live only on suitable bacteria. The phages are thought to be much smaller than most viruses, probably from 25 to 60 mμ. Because both the viruses and the phages have very specific properties and reactions with their respective hosts, it seems logical to infer that they have definite organization and the ability to transmit their characteristics to their offspring perhaps by means of genes. The fact that the known phages and viruses depend upon other organic forms higher in the scale of life as sources of food material may be advanced as an argument against their having preceded the higher forms in time. It is a valid objection. Two escapes from the dilemma are possible: (1) that earlier forms of phages and viruses were not so limited but endowed with the power of subsisting on simpler organisms, compounds, or directly on inorganic materials and (2) that the present parasitic forms of phages and viruses are simply examples of these general classes of organisms which have changed from earlier habits into that of being parasitic on higher forms.

Recently an American biochemist, W. M. Stanley, succeeded in crystallizing the virus of tobacco-mosaic disease. Other viruses have since been secured in a crystalline or partially crystalline form. Various nonliving materials like cane sugar as well as complex proteins and enzymes also have the property of forming crystals. Protein molecules scale down to around 4 mμ, whereas starch and sugar molecules are thought to be of about 2 and 1 mμ, respectively. From this point, we proceed down to individual atoms of unknown size and finally reach what is considered to be the basis of all matter in the universe, protons, electrons, and neutrons.

The best guess at the moment seems to indicate that under suitable conditions various elements and compounds on the surface of the earth or in the warm seas became organized into very simple forms of living material with the power of nourishing and reproducing themselves. Very likely this process occurred in a variety of places, and, for all we know to the contrary, this form of spontaneous generation may still be going on. The materials so formed were probably relatively stable, but with a tendency for polymerization as well as for various rearrangements of their atoms and molecules to produce somewhat different forms. From these earliest living forms, there perhaps eventually came to be organizations of materials resembling the gene.

Existing singly at first, the genes perhaps gradually combined and took on a protective covering resembling at this point chromosomes. Later, cytoplasmic materials and a cell wall may have been added, and after a few hundred million years development may have reached the one-celled amoebalike stage. Growth, aggregation, variation and differentiation, and specialization of function proceeded, yielding finally the

hundreds of thousands of plants and animals that at present inhabit the earth. It hardly seems necessary to say that we need not expect to find traces of the earliest forms of life, because they were too small for us to see and also because of their fragile nature. The developmental process, then, may perhaps logically be thought of as progressing from the elements to organic substances, to genes, to chromosomes, to single-celled, and finally to multiple-celled organisms and plants.

One-celled to More Complex Living Forms.—It is beyond the scope of this chapter to do more than point out the general road that progressive development apparently has traveled. The first step was perhaps the formation of various hydrocarbons. Next may have come the conversion of the above-formed carbohydrates into an amino acid by the addition of nitrogen and the conversion of the amino acids into a protein through fusion of many amino-acid molecules into one finally complex molecule. Somewhere these minute and relatively simple molecular aggregates must have become endowed with "life," especially in the sense of being able to reproduce themselves as the genes apparently do today.

The reverse of the process described in the previous section might lead from this genelike structure to a microscopically visible one-celled organism after the passage of hundreds of thousands of years. From this one-celled stage we pass to a colony of cells such as the Gonium, or free-swimming colony of 16 cells, or Volvox, in which the cells are arranged in a hollow sphere with (1) division of labor and (2) differentiation into soma and germ cells. The next step is the invagination of one side of the hollow-sphere stage forming a hollow sack two cells deep with the outer cells specialized for locomotion, sensation, and protection and the inner ones for digestion. Here the same opening serves as mouth and vent. Next we find the opening continuing through the body with a separate mouth and vent. Segmentation has taken place, the worm being an example of this stage.

Now we pass to the forerunner of the vertebrates with well-developed gill clefts and an outpouching of the gut region which will one day produce the notochord and eventually the backbone of higher types. The cartilaginous ring at the mouth of the fishes gives us our first indication of jaws, although the vertebrate jaw develops from the first set of gill bars. We also find here our first true division into two sexes, which will persist right up through the higher animals, including man. Here we should mention too the Dipnoi, or lungfishes, which are intermediate between the fish type and amphibian, though they have only a two-chambered heart. The first land-living forms are believed to have come from the lobe-finned ganoids, which like the Dipnoi had an incipient lung.

Amphibians such as frogs and salamanders now appear. They spend their early life in water and later life on land. They have a three-

chambered heart and, in place of fins, five-fingered limbs connected to the body by pectoral and pelvic girdles. After them come the reptiles, some gigantic in size though so well-adapted to their environment that they could not change when it did and so became extinct. Here the gill clefts are still retained in the embryo but the young have lost gills, and the eggs are laid on land rather than in the water. In the higher forms, traces of the fourth heart chamber appears.

From this reptilian type were developed both bird and mammalian forms. Archaeopteryx was a primitive bird type in which the teeth were still retained and the three fingers of the forelimbs were still distinct and used for climbing. In modern birds the teeth have been lost, and the fingers are united by a web. At the summit of the tree of life comes the Mammalia, to which class man himself belongs.

The lowest mammalian forms are those like the spiny anteater and duckbill mole. In these forms the egg is still laid outside the body and the digestive tract and urogenital organs empty into a cloaca as in reptiles and birds. Hair has now replaced scales, and a diaphragm separates the abdominal from the thoracic cavity. The brain is not deeply wrinkled as yet, and the nutritive glands are scattered over the belly region of the female and give out a fluid that is licked up by the young.

The second stage in the mammalian group is represented by the marsupials, such as the kangaroos and opossums. The young are born immature and are placed in a pouch on the mother's belly where they complete their embryonic growth. These species are viviparous and have separate openings for urogenital and alimentary tracts as well as a distinctly four-chambered heart.

The highest stage that the process has yet reached is that of the placental mammals. In these the embryo is retained for a longer time in the mother's womb and connected to the mother for nourishment at the placenta. Here the brain is more convoluted or creased. The mammae, or teats, are well-developed for suckling and arranged over the belly region usually in two rows, although in the highest types they become restricted to the breast region. Representative types here are the ungulates or hoofed animals such as horses, cattle, sheep, swine, etc., the carnivores such as cats, dogs, wolves, tigers, etc., rodents such as rats, squirrels, etc., anthropoids such as apes, gibbons, gorillas, orangs, chimpanzees, and, finally, man himself.

In the anthropoids we find a continued shortening of the snout region and the gradual assumption of an upright position, first evidenced through the use of the arms in swinging in the trees. The increasing size of the brain further shortened the snout, caused the further arching upward of the skull, and eventually threw the face into a similar plane to that of the vertebral column. The gorilla spends most of his time in the trees,

although he does walk clumsily on his hind legs, but his long arms touch the ground frequently—a necessity if he is to keep his balance. The gibbon, a more primitive form than the gorilla, also walks on the hind legs and uses the arms for balance.

The upright position largely frees the front legs from supporting the body and enables the hand to develop as a grasping organ, to pick up and examine food, and to bring it to the mouth, which is now so greatly flattened that it is not so well-suited for picking up food as in long-snouted animals. This also frees the hand for development as a tool-using member, and even the higher apes are able to learn to use simple implements wielded by the hand. The baboons frequently use sticks to pry up stones in search of food. Chimpanzees use stones to crack nuts and sticks to pry things they cannot move with their fingers.

Organic Evolution.—The process sketched in the preceding section is generally known as *organic evolution*. By definition it is "the theory that the various types of plants and animals have arisen by descent with modification from other pre-existing types." Because man is apparently one of the latest products of the evolutionary process, our evidence for it is indirect. From the researches of physicists, chemists, paleontologists, and biologists, we can assume that matter in our solar system has progressed through a succession of stages from electronic to atomic to molecular to colloidal-organic to living forms. The most interesting phase of the process from our standpoint is the development of mind. This arose gradually and has reached its highest present level in man. It has provided the means for increasing control over and independence from the environment and at last enabled us to catch a glimpse of the processes of the universe. Contrary to some opinion, as our knowledge broadens, our reverence deepens.

This view is diametrically opposed to the supernatural theory of separate creation of each species or breed. We cannot here go into the philosophical implications involved in these two contrasting theories. Each individual should think out his own philosophy of life rather than accept some one else's. There are two doors leading into the office where the writer is now working, and, although from a scientific standpoint, it might be important to determine which door one used for entrance, after all, it is not a very important moral or ethical question whether one entered by one door or the other. That one arrives at his destination is certainly of greater ethical importance than his method of travel. The mystery, as well as the beauty, of life is here with us now and we are part of it. How these qualities and we ourselves arrived we do not exactly know, and perhaps we never shall. The question as to who made the universe and why may finally prove to be rather overlarge for our human faculties, but this need not necessarily plunge us into a state of cynicism,

boredom, peevishness, or hostility. We are not here concerned with the question as to "why" life is now found on this planet; nor are we primarily concerned with its mode of origin or its ultimate end. The first and the last of these questions rightfully belong to the field of philosophy.

Science, which is but another name for organized knowledge, is concerned with the mode of origin of living things, but as yet it has no definite answer to this problem. The theory of evolution accepts life as a fact and tries to trace its course through the ages. Once given a living entity that is not immutable but rather prone to vary, the task of the biologist is to ascertain the causes of variation and finally to shape and to mold them to more desirable human ends.

The concept of an evolutionary process is not new for in its broad outlines it was sensed by early Hindu and Greek philosophers. They merely had the vague notion but were able to adduce no proof. The early fathers of the Christian Church seem to have been rather liberal-minded men, but the dogma of the special creation of species and the literal interpretation of the Mosaic account of creation soon came to be the accepted belief. During the difficult Middle Ages, little or no thought could be devoted to questions of this nature. There are occasional references to the general subject in the later writings of men like Bruno, Francis Bacon, Leibnitz, Linnaeus, and Kant, although most of the men of these times who thought about the matter at all believed in the separate creation and the immutability of species.

Buffon (1707–1788), a French naturalist, greatly enlarged the concept of mutability through direct environmental means, an idea which he developed in later life after having earlier subscribed to the idea of immutability. He is a precursor of Lamarck and perhaps also of Darwin in regard to pangenesis as well as the struggle for existence and the survival of the fittest. Coupled with his idea of change due to environmental influences was his further implied belief that these so-called "acquired" characters were heritable. Buffon's chief part seems to have been that of suggesting broad new vistas, rather than filling in details, asking questions for his followers to answer, or opening up new fields for conjecture and experimentation. To him goes the credit for beginning the consideration of organic development from the observational and inductive standpoint.

Erasmus Darwin (1731–1802), an English physician and poet and a grandfather of Charles Darwin, is one of the most imposing figures in this field of human inquiry. He borrowed and enlarged on many old ideas concerning evolution and made distinctive new contributions of his own. He was the first to stress the idea that evolution has been operating from the time of the first primordial life. To him new forms were but the flowering of potentialities originally deposited in the life stream by

the Creator and called into being by the necessity for adaptation. He foreshadows the work of his grandson Charles in allusions to man as an offspring of lower quadrupedal ancestors, in some of which the thumb had accidentally come to lie opposed to the fingers, giving a hand that led finally to the great development of the human mind. He assumed a simple living filament endowed with irritability and sensitivity as the progenitor of all that lives. The first living material was endowed with potentialities for new developments that were called out by the organism's response to pleasure and pain. He followed Buffon and anticipated Lamarck in his belief in the inheritance of acquired characteristics.

Lamarck (1744–1829), a French botanist and zoologist, can be rightfully called the father of the modern theory of evolution owing to his having been the first to devise a phyletic tree to include all plants and animals. He was the first to state that all animals formed a branching series of related forms, shading into each other but with many gaps due to the intermediate forms not yet having been discovered. He believed that small masses of mucilaginous matter took on living properties and became elemental plants or animals. His theory of evolution propounded in 1809 had three main points: (1) that the environment, directly in plants but indirectly in animals through the medium of the nervous system, calls out changes in the organism, (2) that the use or disuse or parts leads, respectively, to their further development or to their atrophy, and (3) that these so-called "acquired" characteristics are inherited.

The main idea to be noticed here is Lamarck's belief that the environment is the principal cause of change. This is similar in its general outline to Buffon's earlier belief that something external to the organism brings about changes rather than something within the organism. Geoffrey St. Hilaire (1772–1844), another French zoologist, subscribed to Lamarck's idea that the environment caused the developmental process but by means of changes brought about in the embryonic or germinal condition rather than in the adult. He thus, in a sense, anticipated Weismann's idea of germinal variation and causation as well as deVries's idea of evolution by means of large jumps or mutations, for his work in the field of teratology made him acquainted with sudden departures from type that, he reasoned, might give rise to new species.

Goethe (1749–1832), the great German poet and philosopher, was, in his earlier days, a scientist working in the fields of botany and anatomy, contributing original papers on the metamorphoses of plants and suggesting, erroneously, that the skull was of vertebral origin. He vigorously opposed the idea of the fixity of species and upheld that of descent with modification, or of the ascent of man from some lower form. In the decade between 1780 and 1790, Goethe provided the beginnings of one of the pillars on which the theory of evolution rests, *viz.*, that of comparative

anatomy and embryology. Osborne yields him the honor of being the first man to conceive evolution in the modern sense and says that the transfer of his affections and abilities to the field of literature retarded the demonstration of the law of evolution by half a century. He first offered the correct solution to the riddle of vestigial structures as remnants of those which were necessary further down the scale of life and foreshadowed the dual nature of the process—its centripetal, conservative, hereditary force and its centrifugal, progressive, variational force.

Cuvier (1769–1832) was a champion of the fixation of species and a stout opponent of transformism. He, nevertheless, was the founder of paleontology, which furnishes still another of evolution's supporting pillars. He explained the series of different forms in the earth's crust as due to catastrophic extinctions and later migrations, whereas some of his students and followers said they were each due to a separate creation. Cuvier's exalted place in the science of his day served to retard the acceptance of the idea of mutability, and his brilliant pupil Louis Agassiz was never convinced of the reality of transformism.

Several noted embryologists of the early nineteenth century stressed the mutability of species and called particular attention to the many similarities between different animals in their early embryonic states and to the fact that the higher animals pass through stages which form the terminal point for lower animals. Many other writers in the first half of the nineteenth century had inklings or convictions about "creation by evolution"; and two of them, Wells in 1813 and Matthew in 1831, recognized the principle of natural selection, which was to form the cornerstone of Charles Darwin's theory as expressed in "The Origin of Species."

Opposition to Mutability.—We should here remind ourselves that in this brief review of the history of men's thinking about animal origins up to the time of Darwin, we have said nothing of the general opposition to the theory of gradual change. True there had been martyrs to this general idea back in the fifteenth and sixteenth centuries, and many others had been forced to recant. The general populace, however, knew little or nothing about such things. Life here was hard for the mass of mankind, but they had what seemed a sure promise of a better one to come. The Roman Church and its Protestant derivatives alike frowned upon any views of man's relation to the universe other than those given in the Mosaic account. So although the general idea of change had had a long history and its development had been contributed to by scores of men for over 3,000 years, yet mankind as a whole was both ignorant of what had transpired and bound by certain dogmas directly antithetical to the idea of evolution. But into this hostile, prejudiced atmosphere the idea did finally come in 1859. It has had a stormy passage but is now

accepted by most educated people, for it seems to offer the best available solution to the age-old problem of the whence of animal forms.

Darwinism.—Charles Darwin (1809–1882), to whom reference has already been made, was an English naturalist. He had been educated in the universities of Edinburgh and Cambridge, studying both medicine and theology. He practiced in neither field, however, and wrote later, "My scientific tastes seem to have been certainly innate . . . I consider that all I have learnt of any value has been self-taught." The foregoing pages will have indicated that Darwin was not the father of the idea of a gradual progressive change. He might perhaps more correctly be called the *attending physician* who brought the conception safely into the world, or as Butler said, "Darwin's chief glory is not that he discovered evolution but that he made men believe in it, and what glory," he added, "could be greater than this?"

Darwin sailed on *H.M.S. Beagle* as naturalist on a round-the-world trip lasting from 1831 to 1836. On this voyage he had the opportunity of studying the rich fauna and flora of South America and several island archipelagoes and was struck by the manner in which animal types shade into each other as well as by the distinctive forms found on separate islands. He began this journey with a belief in separate creation, but the facts he observed caused him gradually to give up this explanation for that of the mutability of species. On his return to England in 1837, he began to collect facts on plant and animal variation and during the next year, while reading Malthus's "Essay on Population," the idea of the struggle for existence that is constantly going on in nature as an explanation of the great variety of plant and animal species came to him as it had previously come to Wells, Matthew, and perhaps many others.

Darwin's thesis involved four points: (1) that organisms vary, *i.e.*, are not exactly like their parents, which no one can successfully deny; (2) that these variations are or may be hereditary, *i.e.*, passed along to future descendants, which again is a commonplace; (3) that there is a continual struggle for existence in nature; and (4) that those best fitted to survive in the given environment will be the most apt to survive and should, therefore, leave the most descendants, which seems to be a very logical assumption. He thought that the working of the above-named four principles would account for the great variety of forms of plants and animals which now inhabit the earth or have inhabited it in the past.

Darwin accepted evolution as a working hypothesis, accepted the obvious facts of variation and hereditary transmission of potentialities, and adduced a tremendous amount of data that seemed to support his thesis that natural selection or, to use Spencer's term, "the survival of the fittest" is the leading actor in this drama of survival. Darwinism is not the process of gradual development itself but is one suggestion as

to how evolution works. Discussions among biologists, therefore, regarding the correctness or incorrectness of Darwinism are discussions regarding the mechanism of evolution, not questionings of the process itself, which practically all biologists and other scientists accept as a very probable—as the most probable—fact.

Darwin saw that organisms vary. He had observed the keen competition to survive in both the plant and animal world, and, when these two ideas are added, the sum is inevitably natural selection. As has been said, the title of Darwin's book should have been the "Survival"

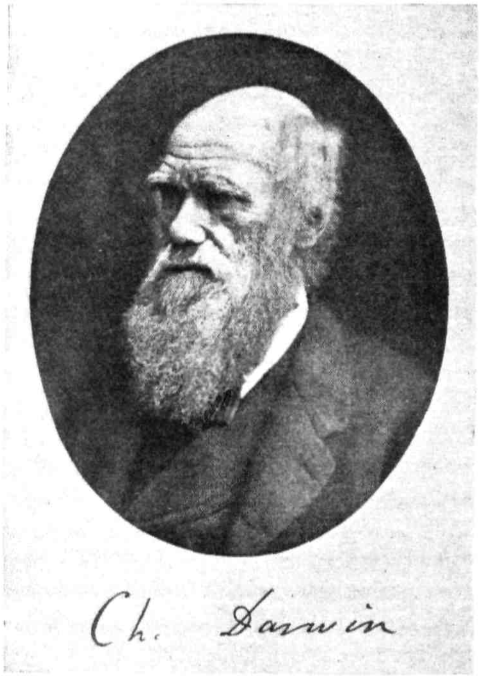

FIG. 23.—Charles Darwin. (*Courtesy of The Journal of Heredity.*)

rather than the " 'Origin' of Species." He accepted variation as he saw it without attempting to explain its underlying causes. He accepted the older ideas of the influences of use and disuse of parts in causing development or atrophy. He concurred in the belief that the environment could cause heritable variations. He made no distinction between germinal and environmental variations. He believed to a certain extent at least in the inheritance of acquired characters and formulated a mechanism for its operation in his theory of pangenesis, *i.e.*, gemmules from all parts of the organism being deposited or registered in the germ cells ready to be passed along to the next generation.

It would have been truly miraculous if Darwin had made no mistakes. Little was known at the time about germ cells and their cytology. Chromosomes, now the accepted bearers of hereditary potentialities, were undreamed of, and naturally the synthesis of cytology and genetics into a firm foundation for biological thought was lacking.

Darwin did not distinguish between genetic and environmental variations but depended on a "strong principle of inheritance" that presumably included both. Later research has shown that the germ cells, ova and spermatozoa, are the bridge of inheritance between parents and their offspring, and numerous attempts to demonstrate the inheritance of acquired characteristics (environmental variations) have failed. Darwin accepted all variations as potentially heritable and was concerned with the mechanism that allowed some variants to survive and breed successfully, whereas others failed. His conclusion was that the environment acted as the selecting agency, preserving some variations while destroying others. This is known as *natural selection*. He built his theory on the cumulative action of a multitude of small variations and looked with disfavor on the possible contribution of big jumps, saltations, or mutations.

Darwin's success was due to his care and patience in gathering facts, a task to which he devoted 25 years, and to his formulation of a workable theory into which the facts would fit. He used the inductive method of science, from facts to general principles rather than the deductive method of principles to facts. He believed that variations occur at random and asked Heaven to "forfend him from Lamarck's nonsense of a tendency to progression or from the slow willing of animals"; in other words, he did not believe in some outside design.

A. R. Wallace, another English naturalist and contemporary of Darwin, reached a conclusion very similar to Darwin's at about the same time, although he had not marshaled so much data to support his thesis as had Darwin and therefore like a true gentleman and scientist yielded first place in this field to Darwin.

Natural Selection.—Thus far no better theory for the appearance of new species has been suggested than Darwin's natural selection among naturally arising variations. Darwin did not try to account for the origin of new heritable variants that might in time become new species. Concern over natural selection, adaptation, and the building of hypothetical classifications probably did much to retard inquiry into the basic facts regarding the origin and mechanism of hereditary variations and their mode of transmission. It was not until the twentieth century, through the synthesis of chemical, physical, genetic, and cytological sciences, that we were to begin to have a clear conception of the basis of living matter and its gradual development through germinal changes.

There have been many attempts to deny the validity of the cornerstone of Darwin's theory, natural selection, and likewise many attempts to replace it with other theories. These in general take two forms: one the substitution of orthogenesis, or progression from natural causes in a straight line, for Darwin's random variation; and the other an appeal to an internal, mystic directing force within the living material.

For the emergence of complex from simple animal forms two things are necessary: (1) living material and (2) some variation. These are obvious to any observing person, and there has yet to be suggested a better selective agency than the one proposed by Darwin. In many species of plants and animals, nature's passive selection has now been superseded by man's active selection. Our task as livestock breeders consists of learning more about the workings of living material, mechanisms of heredity and variation and of devising systems of breeding and selection so that the inherent possibilities of our stock may have the opportunity to make themselves manifest.

Evidence for Evolution.—Lack of space prevents a lengthy discussion of the various lines of evidence which seem to indicate the validity of the general theory of evolution. In outline, they are as follows:

1. *Classification or Taxonomy.* The fact that all the 800,000 described species of animals can be arranged into 11 phyla and the 250,000 known species of plants into 4 phyla, the whole resembling a branching tree.

2. *Comparative Embryology.* The fact that all embryos start as single-celled zygotes, progress along similar lines of development, and that those of the higher species pass hurriedly through stages which are the end product of organisms lower down the evolutionary scale.

3. *Comparative Anatomy.* The fact that the brain, heart, and other organs show a progressive development from lower to higher species, that all mammals have the same bony framework, the bones in the flipper of a whale, the wing of a bird, the front leg of a horse, and the arm of a man being similar in general form and articulation.

4. *Vestigial Structures.* The fact that man during his embryonic life develops a set of gill clefts and arches, a tail, and a fairly heavy covering of hair, all of which disappear before birth, and that adult man has ear and tail muscles, an appendix, and many other vestigial structures which are well-developed and functional lower down the animal scale.

5. *Paleontology.* The fact that fossil remains of animals show a progressive development from lower to higher in ascending strata of the earth's crust.

6. *Zoogeography.* The fact that species grow increasingly divergent in form in widening circles from their point of origin.

7. *Blood Tests.* The fact that the blood of closely related animals shows small incompatibilities as measured by amount of precipitation, whereas distantly related ones show great incompatibilities.

8. *Observation and Experiment.* The fact that all of our breeds of farm animals have been made by a process of selection during about the past 200 years and that recently a successful cross was made between the radish and the cabbage giving a true breeding form having some characteristics of both parents but no longer being fertile with either parent.

Evolution of the Horse.—The evolution of the horse is more completely known from fossils than is that of any other species of animal. Evidences of horses are found in both the New and Old Worlds as far back as Eocene time. Loomis, the leading American student of the fossil horse, held that the species arose in Western North America and migrated across what is now Bering Strait into Asia and Europe. They were once populous in South America as well and have been completely wiped out in both continents at different times. Prehistoric horses were very abundant in both North and South America but were not present here when Columbus made his discovery of this continent.

The American representative of Equus in Eocene times was Eohippus. This was a small animal 10 to 20 in. tall, with four toes on the front feet and three toes on the hind feet. The horse representative of the Oligocene was Mesohippus, a three-toed horse, standing about 24 in. high. On through the Miocene, Pliocene, and Pleistocene, the evolutionary process reveals successive adaptations to perpetuate the species from the standpoint of both nutrition and reproduction.

As the horse changes from a denizen of the swamp to that of the forest and later to that of the open prairie, his teeth grow longer, stronger, and more roughened to suit the gradual change to harsher grasses. Accompanying this change comes a great change in the structure of the feet and legs. The cannon bones, metacarpals and metatarsals, lengthen, the middle toe grows larger and stronger, and the other toes gradually disappear. This permits greater and greater speed, on which this species had to depend for survival. In the modern horse, only the middle or third toe remains, with rudiments (splints) of the second and fourth toes. The Eocene horse with four toes recounts the first of these changes. It is confidently hoped the original five-toed horse will one day be discovered. Figure 24 shows the progressive changes in the teeth and forelimbs of the horse from Eohippus to the modern Equus.

Mechanism of Evolution.—Granted living forms, capable of survival and reproduction, and granted relative but not absolute stability, an evolutionary process would seem to be inevitable. The obvious question at this point would appear to be, what is the mechanism of the process, how did it work? The answer logically involves two factors, one

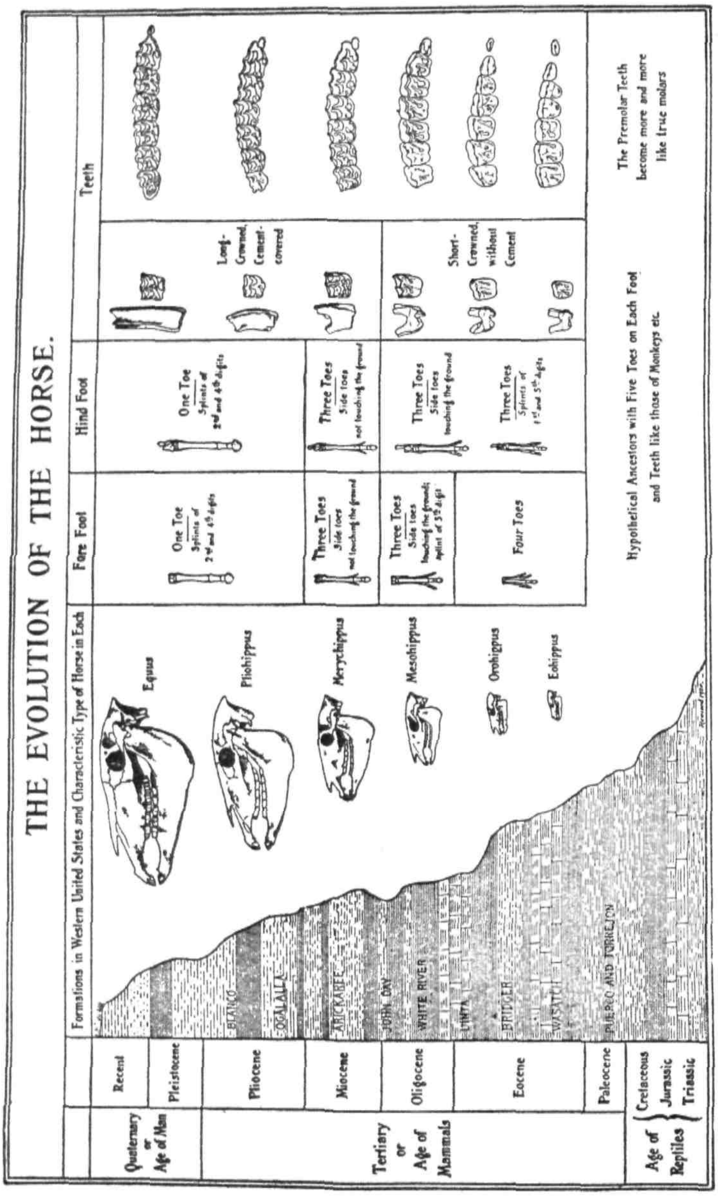

FIG. 24.—Showing progressive changes in skull, feet, and teeth of the horse. (*From Matthew, Quarterly Review of Biology, Williams & Wilkins Co.*)

the internal features and the other the influence of the external environment.

We have assumed that life originated in minute and relatively simple forms. Because the modern science of genetics has shown that inheritance at the present time depends upon the make-up of the chromosomes, meaning thereby their content of genes, it again seems logical to suppose that this has been the system of inheritance from the very origin of life onward.

We do not at the present moment know the chemical content or structure of any gene. After proper staining, the chromosomes in all the higher species can be readily observed. These bodies always have a definite form and number in each species. They appear superficially to be made up of units strung together much like beads on a string. These individual units are the genes. Studies of the giant chromosomes found in the salivary glands of *Drosophila melanogaster* when in the larval stage have shown that the genes are discrete bodies or regions of the greater whole, the chromosome. Cytological investigations have revealed also that demonstrable departures from the normal in mature pomace flies are correlated with evident changes in the form or arrangement of the discrete units making up the chromosomes, the genes. These and many other features of correspondence between genetic development and cytological form will be discussed later when we discuss the chromosomal theory of inheritance. Suffice it to say here that this evidence has now reached the point where it can no longer be doubted. In other words the modern breeder now has a workable theory of inheritance whose broad outlines appear applicable to all forms of life and whose details have already been worked out in many of the lower, simpler, more rapidly multiplying forms. And this theory rests solidly on the genes as the hereditary units involved in the transmission of potentialities from parent to offspring.

The mechanism of inheritance between individuals today is the gene. The mechanism of evolution, inheritance between all living forms in all time, is undoubtedly also the gene. For this to be true the gene must be able to reproduce itself exactly. It does this today at every cell division, it has done it billions of times in your own body, it has undoubtedly been doing it since the earliest living forms first appeared. In addition to reproducing itself exactly, the gene must also be capable of occasionally producing some slight change as it reproduces itself. This power has also been demonstrated in today's living forms, and such changes have been given the name *mutations*. There would seem to be no right or necessity for denying this power to living forms from their very inception.

This, in brief form, is the content of modern evolutionary thought. In other words, its mechanism is to be found in changes in the genes. Of necessity, only those changes which were relatively slight would survive. Any living form, from a single gene to a horse, is a very delicately balanced mechanism. Any major change would probably be lethal. A horse's legs might grow a little longer, and, if this little was not too much to prevent the mouth from reaching to the ground, the horse would survive; if too great, it would be handicapped in securing food. Likewise, small changes in genes are possible of survival, large ones probably not. The gene or the horse can adapt itself to small changes, not to large ones. In time, the summation of many small changes would, of course, cause the organism to vary considerably from its original state. This will be recognized as the heart of the Darwinian theory of the origin of new forms. It is still the most logical explanation of that process.

The stream of life is, therefore, the germ plasm, and the germ plasm is the sum of the genes. Perhaps the genes existed first as naked bodies, next became grouped into aggregates, next took on cytoplasm to assist in their growing complexity of function. We might liken the whole process to radiating assembly lines. The hub or core is the simplest living form, the gene. One assembly line adds but little material as the genes pass along it, and there eventuates at the end of the line an amoeba. Another adds more and different materials, so that there roll off this line marine forms like fish. Yet another line produces amphibia, another reptiles, another birds, and yet another mammals. The workers along these assembly lines are the genes, their raw materials chemical elements or compounds, their finished products all the millions of forms of plants and animals that have lived or exist now.

Role of the Environment.—The other feature of this general problem of the mechanism of evolution is concerned with the environment. Various roles have been ascribed to this feature in the past. As noted earlier, Lamarck and others before and since his time have given first place to the environment as the causative factor of variation. That the environment may have been very active in causing variations in the minute and relatively naked early living (germinal) material seems quite probable, after the hereditary material had encased itself in a protective coat of cytoplasm seems less likely. Just where the dividing line may have come is hard to say. Recent research has shown that the germ cells of forms like *D. melanogaster* are highly subject to change due to direct treatment by varying dosages of X rays or of heat. It seems unnecessary to doubt that the relatively better protected germ cells of higher forms might be subject to similar experimental influences, though perhaps to a lessened degree. That the germ cells can be changed by

such processes seems well-established, that the changes can be induced in an advantageously directed manner is not established. Owing to the delicate balance between any organism and its environment, most of the changes seem to be deleterious rather than beneficial.

The general role of the environment, at least in later stages of the developmental process, seems to have been that of a passive selective agent rather than the direct causative agent. Probably both natural genetic variability and that induced by the environment have functioned from the start. In its earlier stages, changes were perhaps more largely due to the environment; in its later stages, mostly to genetic variations, natural changes in the genes, although for any variation there is presumably some specific cause. This natural genetic mutability is capable of at least two sorts of explanation. Either it is induced by some outside supernatural force, or it is inherent in the relatively unstable nature of the material itself.

The mechanism of inheritance is to be found in the germinal materials, the genes. The process of progressive change is best viewed as that of interactions between the genes and their environment, both cellular and general. In the higher forms, the environment seems to act largely in a passive manner, somewhat perhaps in the nature of a sieve, allowing some varieties better fitted for their particular environment to survive and leave offspring, whereas others are unable to do so. It also seems plausible to think that variations in a certain direction might lead to still others in the same direction, a view known as orthogenesis. The last man born arose through a gradual developmental process beginning as one undifferentiated zygote, ending as an organism made up of billions of cells organized into a definite pattern that sets him off from all his fellows as a unique individual. Logic as well as fact, as far as known, dictate that the first man was made by a similar process.

Mechanism of Development.—Any organism, plant or animal, is composed of cells, one, hundreds, thousands, or billions. In the year 1665, Hooke observed the cellular structure of cork. In 1838, two German scientists, Schleiden and Schwann, propounded the cell theory for both plants and animals. In its very briefest form, the cell doctrine states that all plants and animals are made up of units called *cells*. In both the plant and the animal kingdoms are found all degrees of complexity from single-celled organisms, like algae and amoebae, to highly specialized structures, such as plants and farm animals, which consist literally of billions of cells.

A cell is a bit of living protoplasm in which are to be found vacuoles, plastids, a centrosome, and a nucleus, the whole sometimes surrounded by a wall and sometimes naked. The really important part is the con-

tent of the cell, the sum total of which is called *protoplasm*. This includes the nucleus, centrosome, and the remaining portion called the *cytoplasm*. The body of any multicellular organism is made up of cells (and cell products) that have arisen through cell division from one original cell called a *zygote*. The zygote is the product of the union of two reproductive cells, *viz.*, an ovum from the female and a spermatozoon from the male.

Following the fertilization of an ovum by a spermatozoon, the resulting zygote begins to grow by means of cell division. This one original cell divides into two cells, these two into four, etc., until the complete organism, consisting of billions of cells in the higher animals, is produced.

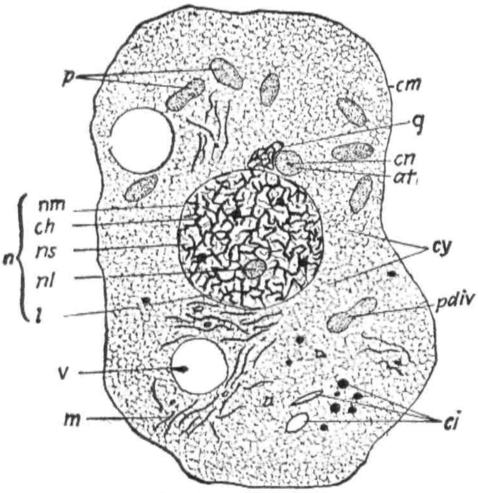

FIG. 25.—Diagram of a typical cell, with structures commonly present. *at*, attraction sphere; *ch*, chromatin network; *ci*, cell inclusions; *cm*, cell membrane; *cn*, centrosome; *cy*, cytoplasm; *l*, linin thread; *n*, nucleus; *nl*, nucleolus; *nm*, nuclear membrane; *ns*, nuclear sap; *p*, plastids; *pdiv*, plastid dividing; *v*, vacuole. (*From Shull, Principles of Animal Biology*.)

The complex individuals found among the higher animals are composed of a great diversity of kinds of cells that have arisen through specialization. All the organs of an animal body are composed of cells more or less specialized in form and function for definite purposes—lung cells for breathing, brain cells for thinking, etc. Reproduction is likewise affected through the activity of certain specialized cells.

Classification of Cells.—For clarity, and because of certain fundamental differences, the cells making up any organism are grouped into two categories. One of these, called the *somatoplasm*, includes all the cells necessary to the well-being of the particular individual whose component parts they are. The other relates to the cells immediately concerned in the production of future individuals and is called the *germ*

plasm. It is essential that the student differentiate clearly between these two. True, the germ cells are housed in and nourished by means of the soma or body cells, but differences in cell division as well as in function place the former in a class by themselves. In farm animals a new individual arises through cell division from a zygote, which is an ovum or egg of the female that has been fertilized by a spermatozoon from the male.

Both ova and spermatozoa are cells with the characteristic cytoplasm and nucleus. The ova are produced in the ovaries of the female. Ova are usually larger than the spermatozoa because of the stored-up food material in the yolk that must serve to nourish the developing individual until the latter becomes firmly attached in the uterus of the mother. The spermatozoa, produced in the testicles of the male, are also specialized for their function of seeking out and fertilizing the ova. They have a characteristic shape, very unlike that of the ova, being made up of three parts, *viz.*, the head, containing the nucleus; the body, containing the centrosome; and the elongated tail, which gives the spermatozoa their motility. The chromosomes found in the nuclei of the germ cells furnish the "bridge of inheritance" between parent and offspring.

Chromosomes and Genes.—The theory was advanced many years ago that certain definite entities in the nucleus of the germ cell brought about the development of certain characteristics in the fully developed individual. Subsequent investigation in cytology has proved the correctness of this hypothesis. In the higher animals, there is a marked distinction between soma and germ plasm, and also between the cytoplasm and the nucleus of the germ cells. It is in the nucleus that the determiners for the individual's characteristics are located. The nucleus itself is made up of two principal parts, the linin network and the chromatin material. This latter goes through various stages in fulfilling its functions. In a resting state, it is strung out in a long thread supported on the linin network. As the cell starts to divide, the chromatin thread shortens and thickens and, finally, breaks up into the number of chromosomes characteristic of the species.

FIG. 26.—Diploid chromosome complement at metaphase in root tip of *Vicia faba.* Spindle-attachment regions of all chromosomes near equator. Nucleolus-forming regions are by the "secondary constrictions" above and below. In this strain one pair of short chromosomes has conspicuous "constrictions" also (left and right). × 1750. (*From Sharp.*)

Each species of plant and animal has a characteristic number of chromosomes. This number is found in the nuclei of all the cells of the body that have a nucleus, with the exception of the germ cells at certain stages as will be noted later. In the human, the number of chromosomes is 48; in cattle, 60; in Drosophila, 8; in corn, 20; and in wheat, 16. The chromosomes themselves are divided into two categories, *viz.*, autosomes and sex chromosomes, the latter being so named because they carry the principal determiners for sex as well as for certain other characteristics. The chromosomes occur in a variety of shapes, though for the most part they are rodlike or oval in shape. Abundant cytological and experimental breeding data have now been diligently studied, and these data have proved that each chromosome consists of a great many constituents known as genes, which are the indivisible units of inheritance.

TABLE 8.—CHROMOSOME NUMBERS IN MAN AND FARM MAMMALS

Species	Number	Authority
Man	48	Evans and Swezy, 1928
Horse	60	Painter, 1924
Cattle	60	Krallinger, 1927
Sheep	54	Berry, 1938
Swine	38	Krallinger, 1931
Goat	60	Berry, 1938

It is supposed that certain of the filterable viruses which are assumed to be the causative agents in certain diseases, such as hog cholera, are composed quite largely of nuclear or chromatin material with very little or no cytoplasm present. As indicated above, it seems most probable that life must have originated in somewhat similar minute bodies and that from this minute origin all the varied forms of living things have arisen by means of heredity and variation. The most logical reason for the differences between individuals would seem to be that their chromatin elements differ. The same is undoubtedly true of species, class, and phyletic differences. During cell division the chromatin becomes stretched out into a long thread, and at more or less regular intervals the thread exhibits regions of thickening. In other words, the chromosomes look like strings of beads. These beads are the genes or factors which bring about the development of all of our individual characteristics. Each chromosome is always reformed from the same group of genes, and each gene always occupies a definite locus on its particular chromosome.

Somatic Mitosis.—Somatic mitosis or cell division is the process whereby one cell, through growth and subsequent division into approxi-

mately equal halves, produces two cells. Somatic mitosis is a continuous process starting with one cell in the resting state and ending with two cells in the resting state. For clarity the process is often divided into four phases, as follows: prophase, metaphase, anaphase, and telophase.

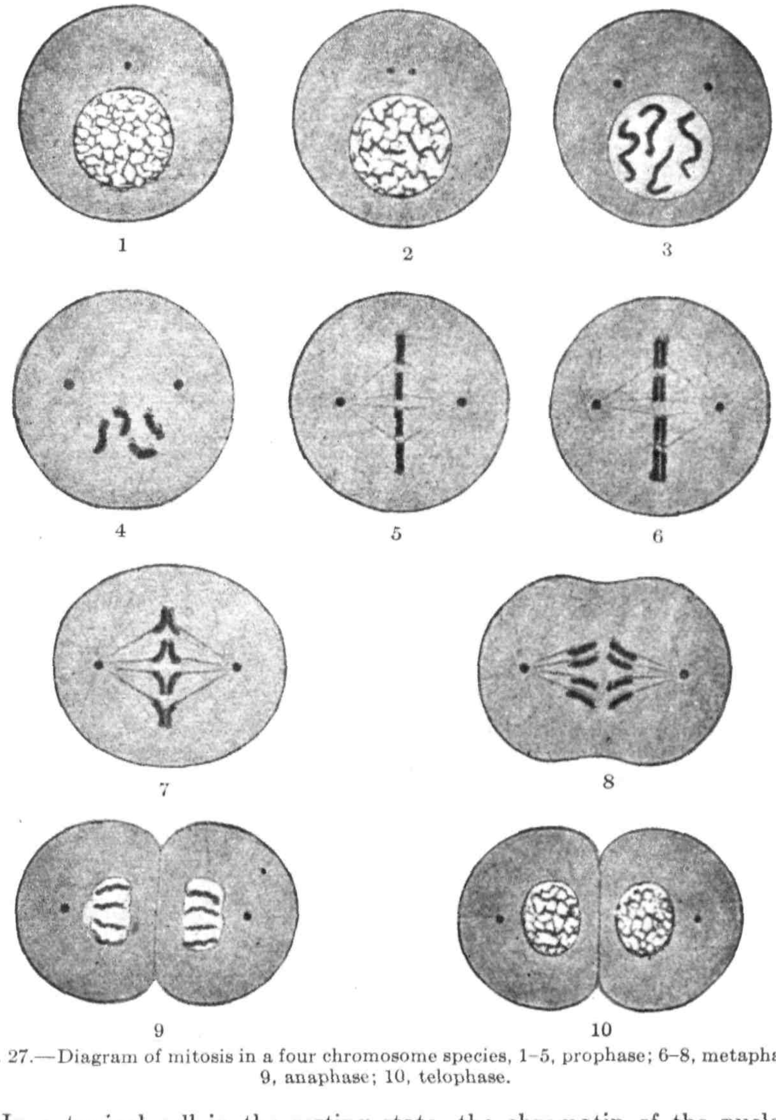

FIG. 27.—Diagram of mitosis in a four chromosome species, 1–5, prophase; 6–8, metaphase; 9, anaphase; 10, telophase.

In a typical cell in the resting state, the chromatin of the nucleus is strung out into long threads presenting the appearance of a tangled skein. In the prophase, a shortening and thickening of the chromatin

and its division into the number of chromosomes characteristic for the species, together with the arrangement of the chromosomes in an equatorial plane, take place. The nuclear wall also disappears during this

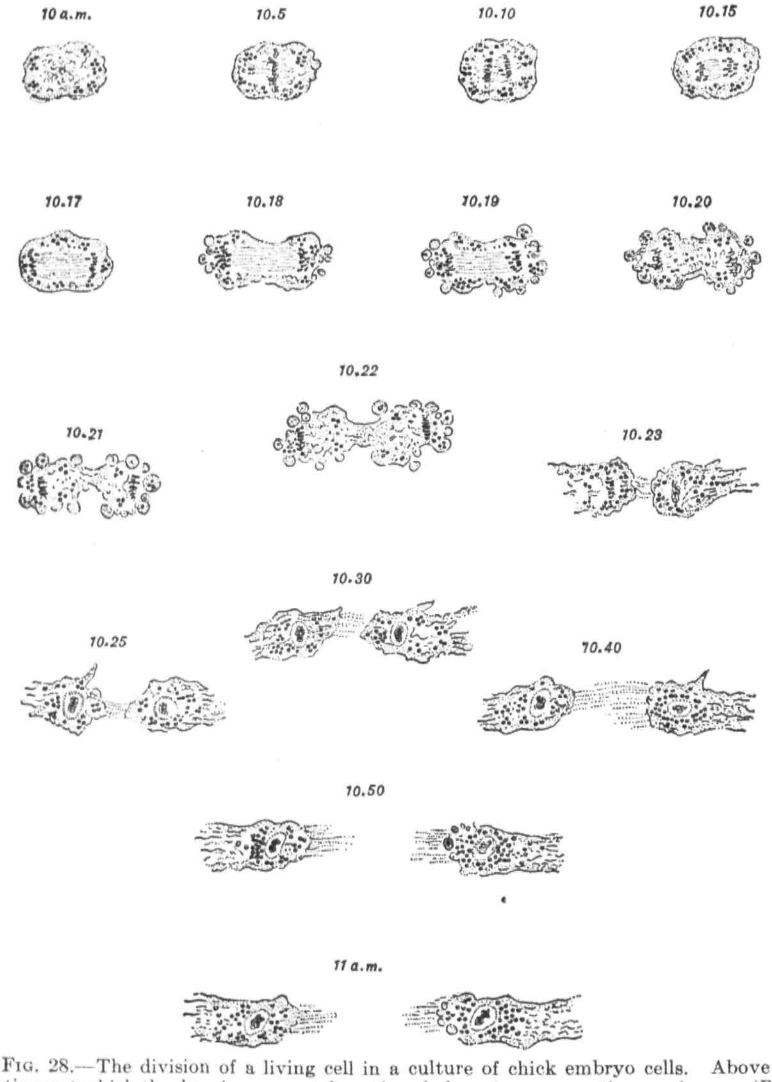

FIG. 28.—The division of a living cell in a culture of chick embryo cells. Above are the times at which the drawings were taken, the whole series representing one hour. (*From C. C. Hurst, The Mechanism of Creative Evolution, The Macmillan Company.*)

preparatory stage. By this time the centrosome, which lies just outside the nucleus, has divided, and one-half of it has proceeded to each pole of the cell with the accompanying arrangement of the asters attached

to the chromosomes. In the metaphase, the chromosomes split lengthwise (or reproduce themselves) into two equal parts, and these parts start to move to the opposite poles of the cell. In the anaphase, the two groups of chromosomes complete their migration, one group to each pole of the cell. In the telophase, the cell wall constricts, forming two new daughter cells, each with cytoplasm, centrosome, and nucleus with its chromatin, in place of the one original parent cell.

Such cell division with differentiation is characteristic of the rise of a many-celled organism from a single-celled zygote. At times this process stops short and a dwarf results; and at other times it continues beyond the normal, the individual with an extra number of cells being a giant. Various types of abnormalities arise from causes unknown. The force that specifies when, where, and how differentiation is to take place is not definitely known. Perhaps it is the result of response to internal stimuli, perhaps to pressure of other cells, perhaps to the influences of organizing centers. Up to the present, differentiation is still largely a mystery, but the wonder should arise not at the fact that occasionally abnormalities are produced but, rather, that the whole complicated process from the one to the billions with consequent differentiation is ever accomplished perfectly.

Origin of Germ Cells.—The mechanism of inheritance resides in the germ cells, the only direct contribution of parents to their offspring in the higher species. The mode of origin of germ cells is a very important consideration. As we shall see in detail in the next two chapters, they are produced in testicles and ovaries, but they should be thought of as direct lineal descendants of the fertilized ovum that has also given rise to the entire somatoplasm of the individual now producing germ cells. At sexual maturity, germ cells will begin to be produced by the germ plasm, but the chromosomes and genes in these germ cells are not derived in the final analysis from the body of the parent (somatoplasm) but from the same source from which the body of the parent has come, *viz.*, the fertilized ovum or zygote.

Summary.—We have tried in this chapter to trace the broad outlines of the process of development of animals from its probable inception in ultramicroscopic forms on up through its varied manifestations to its final eventuation in the highest mammals. We have tried to correlate the processes of heredity and variation, as we know them to manifest themselves today in our breeding animals, with the greater process of the production of new species and races. We have seen that life apparently first manifested itself in some very simple forms, and that by means of heredity and variation plus differential survival all the thousands of higher forms have gradually made their appearance in an orderly progression. Thus it has appeared that all living forms are related, or,

if not all tracing back to one original living thing, they all must trace back to similar original manifestations of life. Finally, we outlined the process of somatic mitosis by means of which a new individual gradually arises from a fertilized egg.

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SECTION II

Mechanisms of Reproduction

CHAPTER IV

THE MALE'S PART IN REPRODUCTION

The science of physiology seeks to explain the how and the why of all the varied reactions or responses of living organisms to external or internal stimuli and to determine the function of each organ of the body, as well as the interrelations existing among all parts of the body. The physiology of reproduction seeks to explain the part that each of the specialized organs of this system plays in the animal's ability to reproduce its kind.

From the time of the early Greeks on through the Dark Ages, the works of Galen, an anatomist of the second century, served as the authority in anatomical and physiological science. This was in keeping with the general tendency of the time to believe what some one else had said, rather than to question and to seek to test whether what was asserted was actually true. Galen used the method of observation but made his observation on animals alone. applying the results in a general way to man.

In 1315, an Italian professor, Mondino da Luzzi by name, published a work on human anatomy based on dissection of human bodies rather than on Galen's authority. It remained, however, for Vesalius, a Belgian born in 1514, to break the allegiance to old authority and to set up experimental inquiry in its place.

After the establishment of the experimental method, in which Harvey, an Englishman, played a leading part, all that remained needful was the perfection of method. Up to the seventeenth century, restricted progress was all that could be expected, for it was not until then that men such as Hooke and Grew in England, Malpighi in Italy, and Swammerdam and Leeuwenhoek in Holland began to develop compound microscopes for study of minute phenomena of all kinds. Physiology is founded upon the function of organs, but it was not until 1838 that men began to understand even the structure of organs. This development started with the founding of the cell doctrine of Schleiden and Schwann in that year.

Preformation and Incasement.—The older thought and belief regarding reproduction were embodied in the "preformation theory." This was, in effect, a theory that the whole body with all its parts was already contained in the egg of an animal but in such a minute and transparent form that it could not be detected and that, therefore, the whole of development was nothing more than a growth, or an unfolding, of the parts that were already "infolded." Closely connected with this theory was that of incasement. According to this theory, the embryonic ovary was supposed to contain the ova of the following generation; these again the ova of the next, etc., *ad infinitum.*

Early Discoveries in Embryology.—Wolff, in 1759, after careful observations, proved that embryonic development did not consist of an unfolding of the preformed organs but was a series of new constructions, one part arising after another, all of them simple in their early stages, though perhaps highly specialized later. The substantiation of his finding by Oken, in 1806, stimulated activity in the field of embryological research. Baer was the most successful of these investigators. His contribution led to the discovery of the three germinal layers on the germ disk of all the higher animals, *viz.*, the ectoderm, the mesoderm, and the endoderm.

From the ectoderm arise later the nervous system, important parts of the sense organs, the outer layer of the skin, and some others; from the endoderm, the lining of most of the digestive tract, and such outgrowths of the digestive tube as the liver, pancreas, and the lungs; and from the mesoderm, the muscles, bones, blood system, and most of the uro-genital system.

Baer also first discovered the human ovum, a tiny cell in the Graafian follicle $\frac{1}{125}$ in. in diameter.

Ten years after Baer had given a firm foundation to embryological science by his theory of germ layers, a new task confronted it on the establishment of the cellular theory, in 1838. What is the relation of the ovum and the layers which arise from it to the tissues and cells which compose the fully developed organism? The correct answer to this difficult question was given about the middle of this century by two distinguished pupils of Johannes Müller—Robert Remak, of Berlin, and Albert Kölliker, of Würzburg. They showed that the ovum is at first one simple cell, and that the many germinal globules, or granules, which arise from it by repeated segmentation, are also simple cells. From this mulberry-like group of cells are constructed first the germinal layers, and subsequently, by differentiation or division of labor, all the different organs. Kölliker has the further merit of showing that the seminal fluid of male animals is also a mass of microscopic cells. Thus it was proved that both the materials of generation, the male sperm and the female ova, fell in with the cellular theory.[1]

[1] HAECKEL, E., "The Riddle of the Universe," p. 58, Harper & Brothers, New York, 1901.

Forms of Reproduction.—From the standpoint of nature, there are three main considerations for any succession of individuals: (1) the individual must be born, (2) it must grow to maturity, and (3) it must reproduce in order that the cycle may be endless. Reproduction is the most vital consideration in nature. It simply cannot fail, and the adaptations to prevent failure are almost endless.

There are two general types of reproduction, *viz.*, asexual and sexual.

Asexual

Fission. Cell division.

Budding. A small part being pinched off.

Vegetative. Regeneration of a whole from a part.

Sexual

Parthenogenesis. Female hatching young from unfertilized eggs.

Paedogenesis. Reproduction by young or larval animals (may be parthenogenetic).

Hermaphroditism. Both sexes in one individual.

Unisexualism. Requiring combined function of two individuals of opposite sex.

In all the higher animals, unisexuality prevails, the union of male and female germ cells, produced by the two separate entities, being necessary for the production of a new individual. All the marvelously specialized organs, in both male and female, for accomplishing this result have had a common origin, and, although the differentiation probably began millions of years ago, there still remain many similarities between the male and the female genitalia. The reproductive organs of one sex have their homologues in the other, although each has been specialized for its respective function. The genital ridge, the first indication of sex organs in the embryo, is much alike in both male and female of the higher species for a considerable time before specialization begins.

It will be the purpose in this and the following chapter to study the principles underlying reproductive physiology. It is not the purpose to attempt to develop veterinarians, however desirable that might be from a breeding standpoint, but to impart to the breeder intimate knowledge of the principles underlying reproduction, in order that he may practice his profession wisely and understand and counsel with the veterinarian when it becomes necessary to call upon the latter.

Embryological Development of the Genitalia.—The urogenital system of the higher animals is formed for the most part from mesodermal tissue. This double system, designed both to rid the body of certain waste products and to provide a means for reproducing the species, has had a very interesting evolutionary development.

The earliest stage in this development results in the formation of the paired pronephric tubules, or pronephros. This is the functional kidney in Amphioxus and some lampreys. It forms in 7 to 14 somites toward the cephalic end of the embryo from the intermediate cell mass of the mesodermal somite (nephrotome). Mesially this forms an invagination opening into the coelom, with which blood vessels communicate and waste products transfuse into these invaginated areas. The free or distal end of this section of each of these somites canalizes, the tubular ends bend backward, anastomose, and form a duct that runs posteriorly and empties into the cloaca, the pronephric duct. These structures are found in early embryonic stages of larval fishes, amphibians, reptiles, birds, and mammals but are transitional.

The second kidney formed is the mesonephros. As the primitive pronephric tubules degenerate, there are formed behind them about 80 mesonephric tubules that empty into the already-formed pronephric duct. This second formation is known as the *mesonephros* or *Wolffian body* and serves the higher organism as a temporary excretory organ, although in man it is entirely degenerate in a four-month embryo. The old pronephric duct is now called the *mesonephric* or *Wolffian duct.* For some larval fish and amphibians, the mesonephros is the permanent kidney.

The true kidney is the third stage in this evolutionary process. The ureter and collecting tubules of the permanent kidney grow out from the caudal end of the mesonephric duct, while the secretory tubules and Bowman's capsule are formed from the caudal end of the nephrogenic cord.

The growth of these tissue in the successive somites of the early embryo causes a longitudinal ridge known as the *urogenital ridge* to form in the body cavity on either side of the median line. This ridge soon divides into a lateral mesonephric fold and a median genital fold. In the former are located the Wolffian duct, already spoken of, and there later forms, by invagination, another hollow tube, the Müllerian duct. The mesial portion of the urogenital fold—the genital fold—is of peculiar interest because it is destined to form either testicles or ovaries. This genital fold in the early weeks of embryonic life extends from near the diaphragm back toward the posterior end of the embryo. Later the anterior portion of the body grows relatively faster, so that the fold assumes a more caudal position, and this together with differential growth causes the genital fold to assume a beanlike shape. Thus are formed the gonads, or precursors of testes and ovaries.

The human embryo, therefore, at six weeks has a pair of undifferentiated gonads and two sets of tubes, Wolffian and Müllerian. Its sex has been previously determined by the chromosome content of the egg

and sperm, but there has as yet been no differentiation of specific male or female parts. Such differentiation begins to be noticeable at about six weeks when the embryo is about 1/3 to 1/2 in. in length.

If the embryo is destined to become a male, the gonads complete their development into testes, which pass down into the pelvic cavity and about a month before birth into the scrotum. The Wolffian duct (old pronephric) differentiates into the long, variously differentiated tube which will eventually carry the spermatozoa from the testes out through the penis. The Müllerian duct on the other hand atrophies and, except for two small vestiges (at the top of the testicle and embedded in the prostate gland), disappears.

If the embryo is destined to become a female, the gonads develop into ovaries, the Müllerian duct into the uterine tubes, uterus, cervix, and part of the vagina, while the Wolffian duct, again except for two small nonfunctional vestiges in the ovary, disappears. In some cases the sex-differentiating mechanism fails to function properly and varying incomplete stages of both sexes appear in the individual, popularly, but erroneously, called a *hermaphrodite*.

The gonad consists of a central core of connective tissue, or stroma, with blood vessels and nerves and is covered with a layer of germinal epithelium. Columns of cells (Pflügers egg cords) from the germinal epithelium grow down into the stroma. In the male these cords give rise to the convoluted seminiferous tubules that after birth canalize into tubules in which the spermatozoa eventually are formed. The sustentacular cells of Sertoli, or nurse cells, are formed within the tubules from the undifferentiated epithelial cells of the sex cords, while the interstitial cells that lie outside and around the tubules are formed from the mesenchymal stroma. After the fifth week, a dense layer of connective tissue, the tunica albuginea, develops between the germinal epithelium and the sex cords, and the epithelium is reduced to a single layer of flat cells.

In the female the process is very similar, except that the first group of egg cords seems to disappear after which another group of egg cords passes down into the stroma of the ovary. These egg cords break up and form the many thousands of immature follicles that are present in the ovaries at birth.

It is seen from the above that the primordial germ cells are present in an embryo at a very early age. Granted normal health, there is nothing that a breeder can do to change them or their hereditary units in any way. From a genetic point of view, an animal will transmit just the same when it is a two-year-old as when it is a ten-year-old. We can trace these early germ cells' precursors in the embryonic testes or ovaries back to the original fertilized egg or zygote that gave rise to

this particular embryo. It is seen, therefore, that the manner in which an animal will transmit is determined very early, actually when the specific egg was fertilized by the specific sperm to produce this specific animal. The new being got certain determiners of hereditary characteristics from both of its parents. At sexual maturity, it will be ready to pass on a sample half of this hereditary material to each of its offspring. After fertilization has once taken place the breeder is powerless to change the genetic make-up of the developing fetus. His only chance for animal improvement comes before this event, and his task is to devise ways of learning the genetic content of the germ cells of his animals so that he may know what he actually has from a genetic standpoint in the animals in his herd or flock.

The germinal tubercle develops in the mid-line between the umbilical cord and anus at about the third or fourth week of embryonic life. On its caudal slope there appears a small urethral groove. In the male this groove closes over, and it eventually extends all the way through the penis and the glans. Rounded ridges (labio-scrotal swellings) appear on each side of the base of the phallus and in the male hollow out to form the two-chambered scrotum or sac in which the testes are carried. In the female the phallus lags in development and eventually forms the clitoris, while the labio-scrotal swellings form the labia majora, or external lips of the vulva.

Testicles.—The primary function of the testicle is that of producing spermatozoa. In most of the invertebrates a simple tube leads from the testicle to the exterior, and, because eggs in these forms are also passed to the exterior by the female, fertilization takes place outside the body. In the higher vertebrate forms, on the other hand, this tube is of considerable length, has a complex organization of several highly specialized parts, including several sets of accessory glands, and ends in an intromittent organ, so that sperm can be deposited in the female genital tract, where fertilization occurs and embryonic development proceeds to completion.

The development and functional activity of these accessory tubes and glands are dependent upon the second function of the testicle, *viz.*, its endocrine function. Internal secretions or hormones of the pituitary and the testicle regulate the development and functioning of the male genitalia in each species of animal. In some species, this stimulation and the attendant production of spermatozoa is constant after a certain age; in others it is intermittent, depending largely on environmental stimuli. Among the latter species are found many fish, amphibians, reptiles, birds, and probably the majority of mammals. In most domesticated and semidomesticated animals, however, as well as in man, spermatogenesis is practically continuous throughout reproductive life,

though at varying rates in youth, middle and old age, and perhaps also at different seasons of the year.

As noted above, the testicles arise from the intermediate portion of the mesodermal somites. They pass into the scrotum, if at all, during the last stages of embryonic development. Their histological develop-

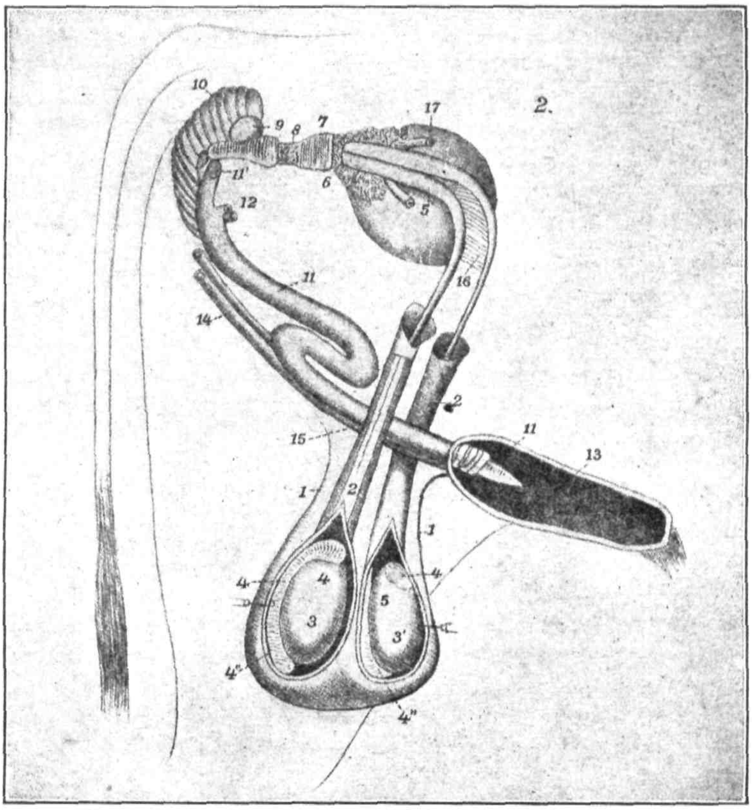

FIG. 29.—Generative and urinary organs of bull. 1, scrotum; 2, spermatic chord; 3, testicle; 4, epididymis (globus major and minor); 5, vas deferens; 6, vesicula seminalis; 7, membranous portion of urethral canal covered by Wilson's muscle; 8, part of prostate gland covered by Wilson's muscle; 9, Cowper's gland; 10, accelerator urinae muscle; 11, penis; 12, cut suspensory ligaments of penis; 13, sheath, laid open; 17, ureters. (*From U.S. Department of Agriculture, Diseases of Cattle.*)

ment following birth has been traced by Phillips and Andrews for the bull and boar. In the bull a marked development of the germinal epithelium was first observed at 142 days with spermatozoa being produced at 224 days. Corresponding figures for the boar were 84 and 147 days, respectively. These workers showed also, as have others, that a low plane of nutrition greatly retarded proliferation of germinal tissue and the appearance of live sperm in the tubules.

The testicles are covered with peritoneum beneath which is a layer of dense fibrous tissue, the tunica albuginea, from which small bundles of connective-tissue fibers pass inward to form the central core of each testis, the mediastinum testis, and in this way the testicle is divided into many small compartments.

The testicles comprise blood vessels, nerves, interstitial, connective, and spermatogenetic tissue. The secreting tissue is located within the

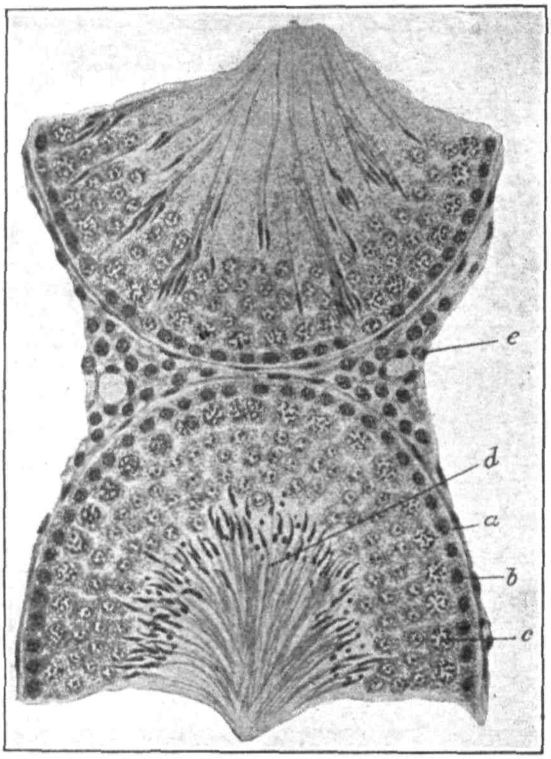

Fig. 30.—Section through seminiferous tubules. *a*, basement membrane; *b*, spermatogonium; *c*, spermatocyte; *d*, spermatozoa in cavity of tubule; *e*, interstitial tissue containing blood vessels. (*From Marshall, The Physiology of Reproduction, Longmans, Green & Co.*)

convoluted seminiferous tubules found within the separate compartments of the testicle. Since millions of spermatozoa are ejaculated by a male at each service, a large amount of secreting surface is necessarily required. This has been ingeniously and compactly provided by nature in the form of the seminiferous tubules. It has been estimated that in one testicle of a boar the seminiferous tubules, if laid end to end, would measure over 3,000 m. or about 10,000 linear feet, whereas in man they would measure 1,000 ft. and in the bull 3 mi. The walls of these tubules

are formed of several layers of epithelial cells, and lying next to the basement membrane is a layer of cuboidal cells, the spermatogonia or sperm mother cells. These cells are direct descendants of the original zygote that gave rise to the organism and very little differentiated from the original zygote. The spermatogonia or sperm mother cells grow and enlarge and may divide to form either other spermatogonia or primary spermatocytes. The spermatogonium remains at the wall of the tubule while the other, the primary spermatocyte, begins to move toward the lumen. This latter cell goes through two rapid cell divisions. Previous to the first cell division, synapsis (fusing of like members of pairs of chromosomes) occurs.

During synapsis each of the fused homologous chromosomes splits or reproduces, each one thus coming to consist of two sister chromatids,

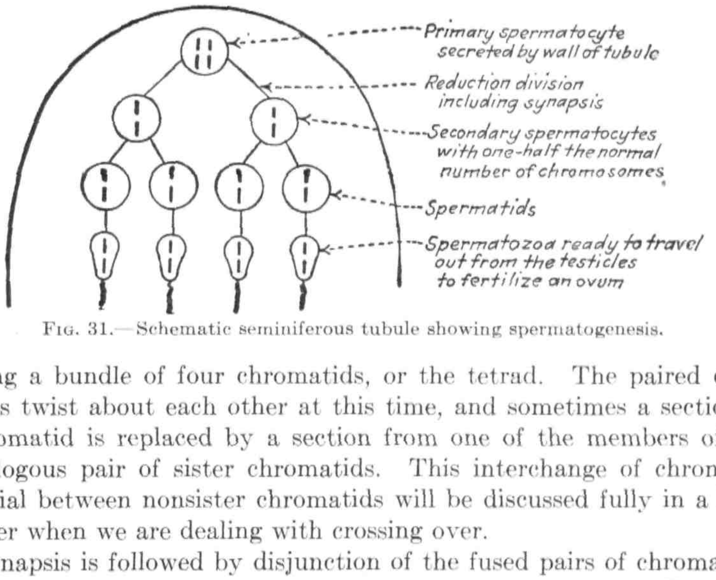

FIG. 31.—Schematic seminiferous tubule showing spermatogenesis.

making a bundle of four chromatids, or the tetrad. The paired chromatids twist about each other at this time, and sometimes a section of a chromatid is replaced by a section from one of the members of the homologous pair of sister chromatids. This interchange of chromatin material between nonsister chromatids will be discussed fully in a later chapter when we are dealing with crossing over.

Synapsis is followed by disjunction of the fused pairs of chromatids, one pair now moving to each of the two poles of the cell. Upon the completion of this migration of chromatids, the cell wall constricts, forming two secondary spermatocytes, each with one-half the normal number of chromosomes for the particular species, each in the form of a fused pair of chromatids. This division is spoken of as the *heterotypic division*, because the two resulting cells are not identical with the parent cell. The two secondary spermatocytes now go through a homotypic division, one of the original four chromatids being found in each of the resulting four spermatids. The spermatids in turn become elongated, the nucleus passes to one end, and the opposite end stretches out into a long filamentous tail, the lashing of which provides the sperm with its

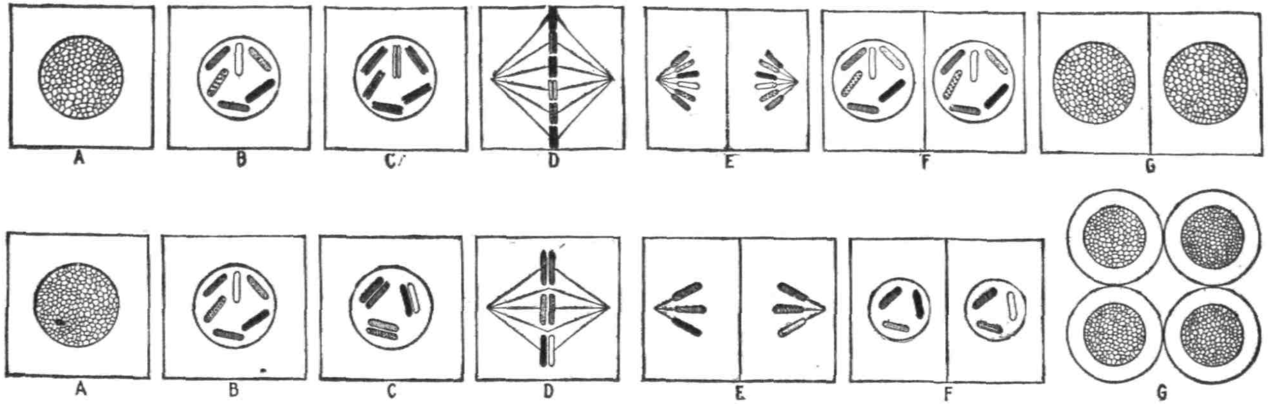

FIG. 32.—Comparison between mitosis in the body cells and in the meiotic divisions which precede the formation of the reproductive cells. The individual chromosomes are differently marked. In ordinary mitosis (upper row) it is evident that the chromatin is divided equally between the two daughter cells (*F* left and right). In the reduction divisions (lower row) the chromosomes do not split but align themselves in pairs (*C* and *D*) and one member of each pair goes to each pole (*E*), resulting in the formation of two cells (*F*), each with half as many chromosomes as the body cells. These by a subsequent mitosis give rise to four functional gametes (*G*). (*After Sinnott and Dunn, modified from Sharpe.*)

motility. The newly formed spermatozoa then become attached to the large nurse, or Sertoli cells, which project toward the lumen of the seminiferous tubules. The fully developed spermatozoa are found eventually in the lumen of the tubules through which they make their exit from the testes.

The convoluted seminiferous tubules become straight and join severally to form the rete testes, from which the efferent ducts, or vasa

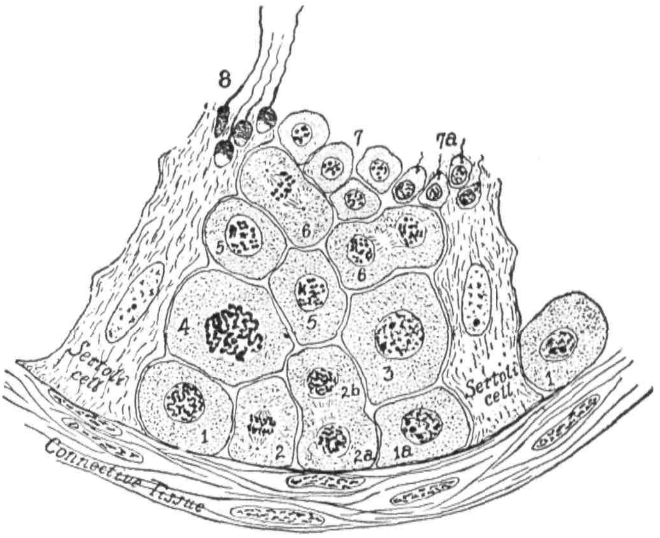

FIG. 33.—Semischematic figure showing small segment of the wall of an active seminiferous tubule. The sequence of events in the production of spermia is indicated by the numbers. A spermatogonium (1) goes into mitosis (2) producing two daughter cells (*2a* and *2b*). One daughter cell (*2a*) may remain peripherally located as a new spermatogonium eventually coming to occupy such a position as *1a*. The other daughter cell (*2b*) may grow into a primary spermatocyte (3) being crowded meanwhile nearer the lumen of the tubule. When fully grown the primary spermatocyte will go into mitosis again (4) and produce two secondary spermatocytes (5, 5). Each secondary spermatocyte at once divides again (6, 6) producing spermatids (7). The spermatids become embedded in the tip of a Sertoli cell (*7a*), there undergoing their metamorphosis and becoming spermia (8), which when mature are detached into the lumen of the seminiferous tubule. (*From Patten, Embryology of the Pig, 2d ed., P. Blakiston's Son & Co.*)

efferentia, which number 15 to 20 in the horse and 20 in man, arise. These in turn converge into one tubule forming the head of the epididymis. The other principal constituent of the testicle is the interstitial tissue (cells of Leydig), which is found packed around and between the seminiferous tubules and which is generally believed to secrete the testicular hormones.

Scrotum.—The testicles are formed in the abdominal cavity, and in some species they remain there throughout life. In the course of evolution they gradually come to lie at the posterior end of the body

pressing against the body wall. A continuation of this process finally led to an outpouching at this region forming a sac, the scrotum, outside the body proper. It is here that the testicles are found in mammalian farm animals. In many other animals (*e.g.*, birds) they remain in the abdominal cavity permanently, whereas still others (*e.g.*, woodchuck) show an intermediate phase with the testicles descending into the scrotum during the breeding or rutting season and being withdrawn into the body cavity when this season is completed.

In addition to serving as a covering for the testicles, the scrotum also functions as a thermoregulatory mechanism. This function of the scrotum is shown by actual differences in temperature, as demonstrated by Moore and Quick, Harrenstein, and Phillips and McKenzie, the temperature in the scrotum being from 1 to 8°C. lower than that of the abdominal cavity. It has been shown by several workers that insulation or the application of heat to testicles results in a degeneration of the spermatogenetic tissue, the production of abnormal sperm, and temporary sterility. These results are also known to follow periods of intense fever. Experimental transposition of the testes to the abdominal cavity leads to the same result, and Fukui has shown that cooling of the abdomen after transposing the testicles retards the rate of spermatogenetic degeneration. If this degeneration has not been too severe or prolonged the testicles recover their spermatogenetic function when all conditions return to normal. Moderate lowering of the temperature of the testicles has been shown to have no deleterious effect on spermatogenesis.

The thermoregulatory function of the scrotum is accomplished through the medium of the tunica dartos muscle, as shown by Moore and by Phillips and McKenzie. This muscular coat consists of fibroelastic and smooth muscle and consists of two layers, an outer layer applied closely to the skin of the scrotum and a heavier inner layer. This muscle is highly sensitive to changes in temperature, drawing the testicles close up to the body in low temperatures and reversing the process in high temperatures. As shown by Phillips and Andrews, the development of the dartos anatomically and physiologically parallels the development of the testes, especially their spermatogenetic development. In other words, the gradual transition of the incompletely developed seminiferous tubules of a newborn animal into fully formed tubules endowed with the power of producing mature viable spermatozoa, which occurs during the first few months post partum, is accompanied by the development of the dartos and its transition into a functional mechanism for keeping the temperature of the testicles within physiologically desirable bounds.

If the testicles remain in the abdominal cavity in any species where they should normally descend into the scrotum, a condition known as

cryptorchidism, they usually[1] lack their spermatogenetic function but retain their endocrine function. In some animals, *e.g.*, the elephant and the anteater, the testicles remain in the abdominal cavity; whereas in others, *e.g.*, most of the rodents and the hedgehog, they descend periodically during the breeding season into the scrotum, whence they are again withdrawn into the abdominal cavity. In the stallion, bull, boar, and ram, the testicles communicate through the inguinal canal with the pelvic cavity, where the accessory organs and glands are located. A weakness of the inguinal canal, which Warwick has shown to be heritable, sometimes allows part of the viscera to pass out into the scrotum, this derangement being known as *scrotal hernia*.

Factors Affecting Spermatogenesis.—There are a great many factors, both physiological and environmental, that affect spermatogenesis. A later chapter will deal with the endocrine influences in the field of reproductive physiology, so that we will here confine ourselves to other influences. As noted above, the season of the year has a marked influence on reproductive manifestations.

Light has been shown by a number of workers to have a stimulating effect on spermatogenesis. This has been demonstrated in the junco (Rowan), starling (Bissonnette), duck (Benoit), and sparrow (Ivanova), (Kirschbaum and Ringoen), (Riley) by using increasing amounts of light to simulate the longer days characteristic of the normal breeding season. Under this treatment the testes increased markedly in size from their quiescent state, and their spermatogenetic functions were renewed out of their regular seasons.

Light treatment has been used on some mammals with similar results, *e.g.* the ferret (Bissonnette), field mouse (Baker and Ranson), and hedgehog (Allanson and Deanesly). Some reciprocal experiments also showed that keeping certain animals in darkness retards but does not exclude the onset of rutting. Many animals that hibernate in darkness emerge in active breeding condition, and some animals have not responded to the light treatment.

Research has shown that the increased or earlier enforced activity of the testes is probably due to the action of light in stimulating the secretion of the gonadotropic hormones by the pituitary gland.

Temperature is known to affect breeding activities in a general way. In the Northern Hemisphere it seems quite likely that the spermatogenetic activity of males of species, like sheep and goats, which breed in the fall is more or less quiescent except during the 2 or 3 months of breeding activity. Work has been reported in this field on several species of fish as well as with some of the smaller mammals, and, although

[1] McPhee, H. C., and Buckley, S. S., Inheritance of Cryptorchidism in Swine, *Jour. Hered.*, **25**, (8): 295–303, August, 1934.

some effects of temperature are indicated, the results are not as yet clean-cut. McKenzie and Berliner report seasonal variations in the breeding activity of Shropshire and Hampshire rams. Although the waves of libido were not regular, there was in general a decrease during the warm periods of the year but little coincidence between libido and spermatogenesis, though the number of abnormal spermatozoa increased during hot weather. Abnormal sperm also increased in number when the rams were kept in warm quarters during the winter with the Shropshires being affected more than the Hampshires. Shropshires showed three distinct periods of sexual activity: highest in the fall, less in the spring, and least in the summer. The Hampshires showed these periods to a much less degree.

Diet has long been known to have a direct bearing both on reproductive as well as general health. From a consideration of calories or energy, we have moved rapidly in the past 40 years through matters pertaining to quantity and, later, quality of proteins, minerals, and, finally, since 1912, we have had to reckon with a growing family of vitamins. For normal health and reproductive accomplishments, the body must be supplied with an adequate amount of food materials containing all the necessary ingredients or elements and organic compounds.

Underfeeding retards spermatogenesis in young animals as well as their body growth, though the growth impulses are not destroyed for considerable periods of time, extending in the rat well beyond the time when normal growth would have been reached. In a mature individual, on the other hand, there is much more resistance to degenerative changes in the spermatogenetic tissue, and such change does not manifest itself until considerable body weight has been lost. This loss of activity and degeneration and atrophy of germinal tissue can be readily restored by adequate feeding.

An insufficient supply of vitamin A in the rat has been shown to lead to atrophy of the testes, a reduction in the size of the seminiferous tubules, and to an inhibition of both proliferation and differentiation of spermatozoa. There is rapid repair when vitamin A is again restored to the diet with full recovery in 2 to 3 months. The results of vitamin A deficiency may also become apparent in the accessory organs of the male, including varying degrees of atrophy and epithelial hardening.

Vitamin B consists of several factors: among them a heat-labile antineuritic factor, B_1, and a heat-stable antipellagric factor, B_2, as well as a growth-promoting substance, flavin. Recent work (Cannavà) has shown that the testes of birds are particularly sensitive to the lack of B_1. The tubules become very much reduced in size, and spermatogenesis eventually disappears. Recovery can be effected in from 20 to 60 days with the inclusion of B_1 in the diet. There is no proof that

mammals are similarly affected by B_1 deficiency, but it is known that such a deficiency caused atrophy of the prostate and seminal vesicles probably as a secondary effect of the inhibition of pituitary activity.

Vitamin C (ascorbic or cevitamic acid), which promotes cellular metabolism and respiration and a lack of which causes scurvy in man,

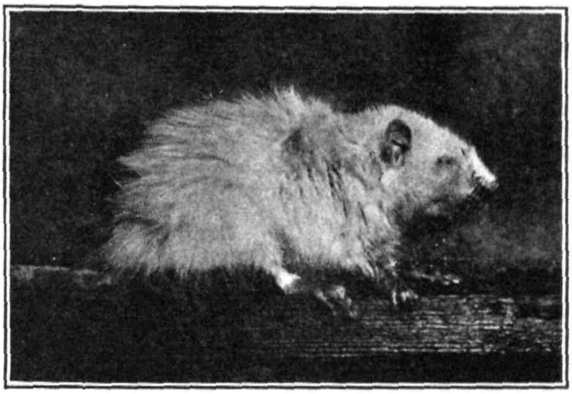

FIG. 34.—A rat showing the effects of a deficiency of vitamin A in the ration. (*Courtesy of Drs. Osborne and Mendel.*)

has been thought, until recently, to have no effect on reproductive efficiency in the male other than a general loss of physical tone leading, in extreme cases, to an inability to copulate. Phillips *et al.* at the University of Wisconsin, however, have recently reported marked improvement in slow-breeding and low-potency bulls through the injection of vitamin C. The treatment consisted of injecting 1 g. of ascorbic

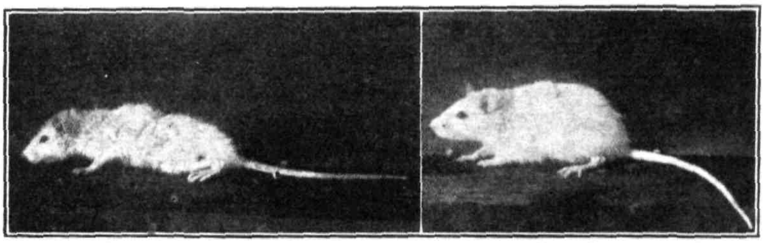

FIG. 35.—A rat before and after receiving a supply of vitamin B. (*Courtesy of Drs. Osborne and Mendel.*)

acid dissolved in sodium-potassium phosphate buffer, physiologic saline or sterile water, twice a week. When so treated, 24 out of 29 bulls showed increased sexual vigor, the quality of the semen was improved, sperm longevity in yolk-buffer solution was increased, and the ascorbic content of both semen and blood plasma was increased to normal. Feeding vitamin C to bulls did not prove effective.

Vitamin D, or the antirachitic vitamin, has not been proved to have any direct effect on the reproductive process. Nevertheless deficiencies of calcium and phosphorus do have a harmful effect on both the reproductive function and lactation. Because vitamin D does either (1) "increase the net absorption of calcium and phosphorus from the alimentary tract" or (2) "help to mobilize phosphorus from sources available within the body tissues," a sufficient amount of vitamin D is seen to be necessary for normal reproductive functioning in the male.

Vitamin E, the antisterility vitamin, is of very great importance for normal reproductive functioning, and fortunately this vitamin is widely distributed in nature, being found in the germs of cereal grains, green vegetables, and animal tissues. Evans and Burr (1927) have listed the following six successive stages of deterioration of functional fertility in the male rat due to lack of vitamin E.

(1) sperm normal in number, morphology, and motility, but fertilizing power lost; (2) sperm morphology normal but motility lost; (3) sperm fused in groups, invested by Sertoli cell "cuffs," and showing abnormal staining reaction; (4) sperm absent in the ejaculate; (5) loss of ability to form the copulation plug, and (6) loss of all sex interest.

The tubules of the rat become much shrunken in size during this process, but there seems to be no change in the interstitial tissue. Unlike other degenerative changes in the testes noted above, those due to vitamin E deficiency are irreversible and when once started continue on to completion. The effect is also restricted to the seminiferous tubules, there being no observable changes in the accessory organs of the male from this cause, and, because these testes with shrunken seminiferous tubules are able to maintain the accessories in a normal state, this is presumptive evidence that the source of the male hormone is to be sought in the interstitial rather than the germinal portion of the testes.

Recently it has been discovered that certain unsaturated fatty acids (linoleic, linolenic, arachidonic) play a part in normal reproductive functioning of the male. Male rats deprived of these constituents lose their sex desire, exhibit priapism, and some degenerative changes in the testes that are repaired when these acids are again included in the diet.

Secondary Sexual Characteristics.—The second function of the testicle, as mentioned earlier, consists of the elaboration of an internal secretion or hormone. This function developed evolutionarily as a necessary concomitant of the lengthening and growing complexity of the tube for carrying the sperm from the testicle to the exterior or to the interior of the female genital tract in order to ensure the meeting

of egg and sperm. The functional states of the various accessory organs of reproduction in the male are dependent on the testicular hormone, as well as is libido, or sex drive, at least to some extent. As mating is seasonal in many species, so likewise is testicular hormonal stimulation. Berthold's classic demonstration in 1849 that successful testicular transplantations into capons resulted in normal male comb growth was the first demonstration of the presence of an internal secretion from the testes. Since 1869, attempts have been made to use testicular extracts for restoring or enhancing masculinity and effecting rejuvenation. These claims for rejuvenation and later ones for changes in metabolic rates and respiration have not been substantiated.

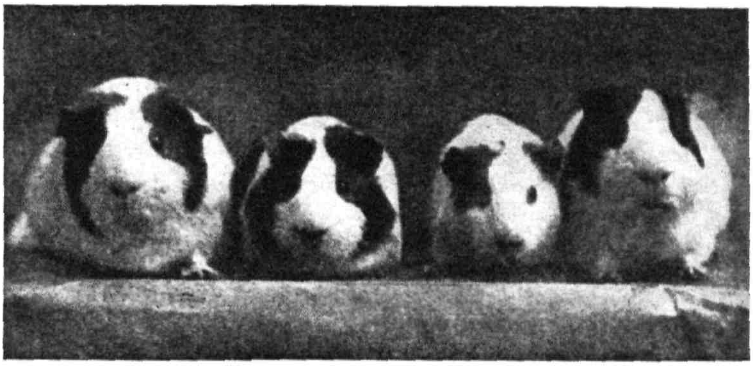

FIG. 36.—Masculinization of guinea-pig. (*From Steinach.*) Reading from left to right, the animals are arranged in the following order: Masculinized female, an ovariotomized sister, a normal sister, a normal brother. (*F. H. A. Marshall, Physiology of Reproduction, Longmans, Green & Co.*)

The male sex hormones are called *androgens*, and their potencies are determined chiefly through their capon-comb and rat-genitalia stimulating effects. The principal known functions of the androgens are to stimulate the growth and physiological activity of the accessory organs of reproduction, to promote sex drive, to maintain a proper general physiological balance of the entire organism through their interlocking relations with the secretions of other ductless glands, to promote the development of the typical secondary sexual characteristics, and perhaps to influence the activities of the testes themselves. The hypophysis secretes a hormone that activates the testes at time of puberty and stimulates them to begin the secretion of viable germ cells, and a secretion of the gonads in turn stimulates the growth of the accessory male organs and causes the body to begin taking on the characteristic male form and attributes.

It has long been known that the characteristic male and female characters are in some way related to the primary organs of reproduction,

testicles and ovaries, because these characters failed to develop following castration in early life. For example, the boar's tusks, the bull's heavy horns and crest, the stag's antlers, the ram's horns, the rooster's comb and spurs are either reduced in size or entirely lacking following castration. The degree of masculinity and feminity is also influenced as well as the psychic characteristics of the individual. The ox is a much more tractable animal than the bull whereas the eunuch, besides having a high-pitched voice, a small chest, and a beardless face, is often lacking in courage, is obstinate, mentally lazy, prematurely senile, etc. It is also known that the full development and functional activity of the accessory organs of reproduction in the male are dependent upon the hormone function of the testicle.

It is well-established that there are correlations and reciprocal relations between the testes and various other glands of internal secretion and these relations will be developed in a later chapter.

Castration.—Removal of the testes and ovaries has long been practiced. In ancient times, men destined for the priesthood were castrated, and it was long the custom so to treat peoples vanquished in wars. Pratt reports that at one time the most intelligent children were castrated and made to serve in domestic duties and quotes Gibbon as saying that, although Rome fell during the time that the eunuchs were in power, the real cause of her fall was the degeneration of her people.

The common method at the present is to remove the testicles after making an incision in or removing the lower portion of the scrotum. This has not always been the procedure, however, as in earlier times it was the custom to crush the testes or to destroy the passage from them by twisting or by tying the spermatic cord.

Many results follow castration: (1) it renders the animal sterile, (2) it improves the propensity to fatten, (3) it improves the quality of the flesh and reduces the proportion of the poorer cuts, *e.g.*, shoulder, (4) it retards the development of the accessory organs of reproduction, (5) it lessens the development of the secondary sexual characteristics, (6) it lessens or removes the desire to mate, (7) it leads to various changes in the other glands of internal secretion, (8) it produces varying psychic changes in animals so treated.

The effects of the testicular hormones are most easily studied in castrates, the comb of birds and the retention of the normal condition of various parts of the reproductive tract and glands in castrates injected with testicular hormones serving as indicators.

Many other claims are made for castration, *e.g.*, the speeding up of the growth process, attainment of greater size, changes in metabolic rates, a lessened activity, a higher degree of intelligence, and a shortened

life. These are still moot questions, and results might vary considerably among individuals and species.

Colts are usually castrated at about one year of age, calves at six to twelve weeks, lambs and pigs at two to four weeks. If castration is planned, it is wise to conform fairly closely to the times suggested above, as it can be performed with less trouble at those ages and with the least setback to the animal. Castration of lambs and pigs is simple and easily performed, though with cattle and horses a veterinarian's aid should be procured until the art is well learned. The cardinal features to be observed in castrating are: (1) to remove both testicles, (2) to locate incisions so as to ensure drainage, (3) to use sanitary precautions, (4) to prevent excessive loss of blood, (5) to do the job as expeditiously and quietly as possible.

Removal of the testicles in farm animals tends to keep the individual's sexual characteristics in the juvenile state rather than to throw them over to the female type. The latter occurs only when ovaries are transplanted into a male. Castration or spaying of the mammalian female does not alter the femine appearance appreciably.

Castration of the male may be performed in various ways. Young pigs are picked up and held on their backs in the lap of an attendant. An incision is made about ½ in. from the median line, the testis squeezed out and the cord severed by scraping. The operation is then repeated on the other side of the median line.

With young lambs and calves—the lambs being held by an attendant, calves often thrown and hog-tied—the lower third of the scrotum is generally cut off, the testis pulled out and the cord broken or scraped with a dull knife until it parts.

Colts are generally left entire until they are about one year of age in order to allow fuller development of the neck, chest, and shoulders. The colt is generally thrown and secured with ropes, an incision made to expose the testes and the cords then crushed with an emasculator.

During the past few years the Burdizzo pincers or emasculatome has come into use. These are double-hinged pincers with tremendous pinching power. They come in various sizes to suit various types and ages of animals. One spermatic cord at a time is caught in the pincers and completely crushed leading to complete atrophy of the testicle in a few months' time. If properly done, the animal is almost immediately sterilized; *i.e.*, spermatozoa can no longer pass up through the vas deferens, which together with the arteries and veins in the spermatic cord have been crushed. However, any spermatozoa in the vasa deferentia above the point of crushing would possibly remain functional for a few days or weeks.

Swelling will persist a little longer in animals that have been castrated by the emasculatome method, but there is generally less shock, less going off feed, and of course practically no danger from infection since no incision is made.

The effects of castration are of course variable, depending to a very great extent on the time at which the operation is performed. If castration occurs early in life, the effects are marked and the accessory organs are prevented from any great development. If performed after sexual maturity, the already formed accessories undergo varying degrees of atrophy.

This concludes our consideration of the primary organs of reproduction in the male, the testes. We will next consider the various male accessories.

Epididymi.—The convoluted seminiferous tubules converge at the mediastinum testes (absent in Equidae) and there join severally to form from 6 to 24 efferent ducts. These in turn unite into one duct, thus giving rise to the epididymis, a greatly coiled tube varying from a few feet to several hundred feet in length in different species. The epididymis is lined with tall columnar ciliated epithelial cells surrounded by a muscular wall, and this in turn is covered by a serosa. One arises near the top of each testes where it is coiled up to form the head of the epididymis. It eventually passes down the side of the testes, in a part called the *body*, to the bottom of the testes where it forms the tail of the epididymis. This tube continues the passageway for the egress of spermatozoa from the seminiferous tubules. Its ciliated cells help to move the more or less dormant and inactive young spermatozoa along, and its cells provide a secretion that perhaps nourishes the spermatozoa. Because the spermatozoa pass through the epididymis at a very slow rate, it also can be called a *storage place* for the sperm.

Breeding tests have shown that sperm from the tail of the epididymis are much more likely to fertilize the eggs than those from the head region, and they become more active as they pass along through the length of the reproductive tube. This is construed as evidence that the spermatozoa are maturing as they pass along the tube. Fluid in the epididymis consists of both testicular and epididymal secretions in which the spermatozoa are being carried. Many spermatozoa probably reach maturity, disintegrate, and are absorbed in the epididymis. Castrated animals, in which a portion of the epididymis remains, will continue to be fertile for several days.

Vasa deferentia.—These tubes are a continuation of the epididymi, continuing the passage for the spermatozoa to the urethra. The walls of the vasa deferentia are thick and consist of layers of mucosa, submucosa, muscularis, and fibrosa or serosa. The lumina are small,

giving the tubes a firm cordlike character. The lining cells are also ciliated. In some species there is an enlargement (ampulla of Henle) near the termination of each vas deferens that serves perhaps as a storage place for the spermatozoa. This is absent in the boar, quite small in the dog and cat, and large in the bull, ram, and Equidae, being over 1 in. in diameter and often exceeding 6 in. in length in the jack. Glands of the vas deferens add to the total content of the semen. The vas deferens together with longitudinal strands of smooth muscle, blood vessels, and nerves all encased in a fibrous sheath make up the spermatic cord (two of them) that passes up through an opening in the abdominal wall, the inguinal canal, into the pelvic cavity.

Vasectomy or exsectioning of the vas deferens is the most usual operation performed on various classes of inmates of state institutions to produce sterility. In the past, many claims for the efficacy of this operation in restoring bodily and sexual vigor have been made. Cutting or tying off the vas deferens was theoretically supposed to result in the atrophy and degeneration of the tubules and a corresponding hypertrophy of the interstitial cells. Numerous experiments and some observations of actually occluded or missing portions of the vas deferens have not substantiated these claims. It seems probable that, if the vas deferens is occluded or cut, local degeneration and aspermatogenesis may result in portions of the testes, but these areas are no doubt cleared up later, the degenerative tissue resorbed, and normal spermatogenesis again renewed.

Ejaculatory Ducts.—These are formed through a union of the vas deferens and the proximal portion of the seminal vesicle on each side. They open into the floor of the urethra through small slitlike apertures between which is found in man the uterus masculinus, or organ of Weber, which is the homologue of the uterus and vagina of the female. In some species, *e.g.*, the boar, there are separate openings for the vasa deferentia and the seminal vesicles into the urethra. On the floor of the prostatic portion of the urethra is found a small elevation known as the crista urethra, or caput gallinaginis, which contains erectile tissues and thus prevents the semen from passing backward into the bladder at time of service.

Seminal Vesicles.—These are the largest of the accessory glands of reproduction in the male. They are located in the pelvic cavity at the ends of the vasa deferentia, being an outgrowth of the latter at their urethral end, and each connects with the urethra by means of a duct.

Miller reports as follows on the seminal vesicles of the boar:

> The glands are tortuous, elongated, hollow bodies, with very irregular, branched lumina and numerous outpocketings. The wall consists of a thin external connective tissue sheet, of a thin middle layer of muscle, and of a mucous membrane resting upon a thin submucous layer. The mucous membrane forms

an elaborate system of thin, high primary folds which branch into secondary and tertiary folds. These project far into the lumen, anastomosing frequently with one another, thereby forming many irregularly shaped cavities of different sizes. These cavities are separated from one another by thin branching partitions, and all opening into a larger cavity.

The epithelium lies on a thin vascularized connective tissue supported by muscle strands. Although showing some variation, the epithelium is simple columnar in nature with some areas pseudostratified. The nuclei are round or oval shaped and located at or near the base. Secretion granules are present above the nuclei and on the free surface, drops or bulblike formations appear. These are cast into the lumen, forming the secretion product. The fluid has a gray, opaque color, a medium viscosity, and a pH of approximately 6.7.

There is no central duct of the seminal vesicles. Instead, there are several large ducts branching and anastomosing irregularly, which finally converge into one excretory duct. The duct from each seminal vesicle enters the urethra as a slit-like opening, close to, but ventro-lateral to the vasa openings.[1]

The seminal vesicles vary in size according to the animal and the species, being in the horse 6 to 8 in. long and about 2 in. in diameter. They are lacking in the dog and cat. The function of the seminal vesicles, although not fully understood, is thought to be the secretion of a fluid that furnishes a medium for transport of the spermatozoa. This secretion is thick, alkaline, and globulin-containing. The vesicles were formerly thought to serve as a storage place for spermatozoa, hence their name, but this theory has been disproved.

Prostate.—At the neck of the bladder, surrounding or nearly surrounding the urethra and connecting with it by two rows of openings on either side of the ejaculatory ducts, is the prostate gland. This gland is a composite of many small compound tubulo-alveolar branching glands. Miller has studied the prostate in the boar and says,

The prostate gland in the boar is a yellowish multilobular gland. It is composed of two parts; the body or bulb, closely attached to the dorso-lateral surface of the pelvic urethra at its anterior extremity, and the pars disseminata which is attached to the body but embedded in the wall of the pelvic urethra beneath the body of the gland. The body of the gland weighs from 15 to 25 grams and measures about 5 cm. in length by 4 cm. across by 0.5 cm. thick. The ratio of prostate body weight to the live weight of the animal was about 1:8,000.

The glandular tissue is firm, without apparent storage space and contains no secretion which can be expelled by pressure. Incomplete sections which have not been made in a known direction, present a bewildering mass of secretory tubules, follicles, connective tissue, smooth muscles, blood vessels, nerves and lymphatics. The gland is a composite of many small compound tubulo-alveolar glands, giving

[1] McKenzie, F. F., Miller, J. C., and Bauguess, L. C., The Reproductive Organs and Semen of the Boar, *Mo. Agr. Expt. Sta., Bul.* 279, p. 36, 1938.

rise to numerous excretory ducts which open into the urethra independently on its dorsal wall.

The prostate is very irregular in form. Large branching cavities, narrow ducts, and alveoli appear to be massed together in an irregular manner. There is no distinct basement membrane and the glandular epithelium rests upon a layer of connective tissue. The epithelium varies from simple or pseudostratified columnar in the smaller alveoli to cuboidal or even squamous in the larger cavities. Numerous secretory granules can be seen in the cytoplasm, and cytoplasmic drops appear to be attached to the free end of the epithelial cells.

There is abundant interstitial tissue which appears to consist of dense connective tissue with collagenous fibers and elastic network, and many smooth muscles arranged in strands of varying thickness. There is also a connective tissue capsule about the periphery of the gland.[1]

The secretion of the gland is viscid and contains proteins and salts, concretions of the latter often causing an inflammation or prostatitis in old subjects. The prostatic secretion is alkaline, tends to cleanse the urethra prior to and at the time of ejaculation, and provides bulk and a suitable medium for transportation of the spermatozoa. In some animals (rodents) the abundant secretion of the seminal vesicles is coagulated in the vagina by an enzyme contained in the prostatic fluid, and thus the ejaculate of the male becomes a more or less solid plug in the vagina of the female.

Cowper's Glands.—Cowper's glands (bulbo-urethral), two in number and corresponding to the glands of Bartholin in woman, are situated in the urethral muscle (except in the boar) on either side of the pelvic portion of the urethra, with which each communicates by means of a small duct. They are lacking in the dog and very greatly developed in the boar, a species in which they may extend the entire length of the pelvic floor and reach a diameter of 1½ in. The function of these glands and the urethral glands is thought to be that of producing an alkaline secretion for the purpose of neutralizing and cleansing the urethra before the passage through it of the main bulk of the semen.

Penis.—The remaining portion of the male reproductive organs consists of the penis. This organ, besides conveying urine to the exterior, has the additional function of conveying spermatozoa into the female genital tract. The penis is made up of muscular and erectile tissue that becomes engorged with blood during the process of erection.

Farm animals exhibit a wide variation in the structure of this organ. In the horse, the end of the penis is rounded, and the organ nearly fills the vagina at copulation. In the bull, the diameter is much smaller, with the external urethral orifice situated in the urethral papilla at the end and on the left side. The urethral papilla of the bull represents a

[1] *Ibid.*, p. 42.

vestigial filiform appendage. This is well-developed in the ram in the form of a slender appendage, which protrudes beyond the glans penis in a twisted manner. The penis of the boar, like that of the horse, is not provided with an appendage or lateral papilla, and the opening to the exterior is situated at the end of the organ and in the center.

During estrus the glands in the female genitalia are active in secreting a viscid fluid. Friction on the glans penis or on the homologue in the female, the clitoris, finally leads to a sexual orgasm that is in part a reflex action, for it can take place after the spinal cord has been transected. Ejaculation by the male is effected by a series of muscular contractions beginning in the vasa efferentia and involving the epididymi, vasa deferentia, vesiculae seminales, prostate, and Cowper's glands. The final discharge is brought about by the rhythmical contractions of the bulbocavernosus and ischiocavernosus muscles, which, proceeding progressively in waves, result in forcing the semen out or ejaculating it from the external orifice of the penis.

Now, in résumé, it may be said that the essential organs of reproduction in the male are the testicles, whose functions are to produce spermatozoa and an endocrine secretion; the accessory glands, the prostate, the seminal vesicles, and Cowper's glands, whose function it is to furnish a medium for the spermatozoa to travel in on their way to impregnate the female; and the epididymi, vasa deferentia, and urethra, the parts of a long tube that provides a passageway for the spermatozoa and in which the spermatozoa become fully matured. The blood vessels, nerves, and muscles function in bringing about erection and ejaculation.

Semen.—Semen is the entire normal discharge of a male at ejaculation. It consists of spermatozoa, along with a small amount of a milky fluid from the testicles, epididymi, and vasa deferentia, and the secretions of the seminal vesicles, of the prostate, and of Cowper's glands.

TABLE 9.—SOME QUANTITATIVE DATA ON SEMEN AND SPERMATOZOA*

Animal	Volume per ejaculate, in cubic centimeters	Sperm per cubic millimeters	Total sperm in ejaculate
Boar	200	100,000	20,000,000,000
Stallion	100	60,000	6,000,000,000
Bull	3–4†	800,000	3,000,000,000
Ram	0.8	1,000,000	800,000,000
Dog	7.0	5,000,000‡	35,000,000,000‡
Cock	0.6	3,000,000‡	1,800,000,000‡

* Adapted from Table 3, p. 36, *U.S. Dept. of Cir.* 567.

† About 1 teaspoonful.

‡ Estimates.

The amount of semen ejaculated varies with the different classes of animals and some average figures are given in Table 9.

Slowtzoff has made comparative analyses of the semen of man, horse, and dog, which have given the following figures:

TABLE 10.—SEMEN ANALYSES

	Dog	Horse	Man
Water	97.560	95.705	90.321
Total solids	2.450	4.295	9.679
Ash	0.687	0.915	0.901
Organic matter	1.763	3.380	8.778
All protein matter	1.259	2.238	2.854
Albumins, globulins, nucleo-proteins	0.886	1.142	2.579 (albumins, globulins, nucleo-proteins and mucin)
Mucin	0.057	0.559	
Albumoses	0.314	0.537	0.412
Lipoids	0.182	0.172	0.208
Cholesterin	0.00075	0.0042	
Various organic substances ("extractives")	0.312	1.090	5.716

Human semen consists, therefore, roughly of 90 per cent water and 10 per cent solids, which, on incineration, yield about 1 per cent ash. About one-fourth part of the solids consists of proteins, of which a nucleoprotein, traces of albumen and mucin, and an albumose-like substance have been identified. The semen of the dog and horse differs in containing more water. This difference is made up by the presence of a large amount of various organic substances in human semen, which have not been clearly identified.

In the ash of human semen, K, Na, Ca, Mg, P, Fe, and S have been found. The quantitative analysis of the ash reveals a remarkably large amount of calcium and phosphoric acid—about 20 per cent Ca and 30 per cent P_2O_5. In man the amount of calcium excreted in one ejaculation is, therefore, about 0.01 gm. and exceeds that contained in an equal quantity of lime water. Analyses of the ash of the semen of other Mammals do not appear to have been made, but it is unlikely that there are any essential differences.[1]

Semen is generally gray to milky white in appearance being lighter colored with higher concentration of sperm. In the boar, McKenzie, Miller, and Bauguess report that 20 to 40 per cent of fresh semen consists of "gelatinous material resembling tapioca." Both the volume and sperm concentration of semen vary between rather wide limits in different individuals and under different conditions. Likewise the morphology, duration of motility, and normality of spermatozoa are variable characteristics and are influenced very greatly by frequency of ejaculation and reproductive and general health. Frequent ejaculations

[1] MARSHALL, F. H. A., "The Physiology of Reproduction," pp. 296–297, Longmans, Green & Company, New York, 1922.

reduce the amount of semen, the sperm concentration, and the duration of motility and may sometimes increase the percentage of abnormal spermatozoa. The above authors cite instances of boars ejaculating 20 billion spermatozoa per day for periods of 11 to 24 days and of one boar yielding 33 billion spermatozoa per day for 14 consecutive days.

Many environmental conditions are known to have an influence on the functional activity of spermatozoa.[1] One of the most important of these is the pH concentration. It has been demonstrated by several workers that the optimum pH for most mammalian spermatozoa is just over or under 7. A slightly acid condition such as exists in the head of the epididymis keeps the spermatozoa relatively immobile. It begins to appear that the presence of other ions may affect the influence of the $H\pm$ ion.

The effects of tissue juices on spermatozoa have been studied by a number of workers. Neither tissue extract from the epididymis nor from the prostate seem to be essential for the life and activity of spermatozoa, the latter in fact shortening the life of the spermatozoa through stimulating them to greater activity. Miller found that, in the boar, removal of the secretions from the seminal vesicles and Cowper's glands not only did not effect a lowering of fertility but actually led to a reduction in the number of abnormal spermatozoa and increased the duration of motility. Vaginal secretions are known to be detrimental to the spermatozoa. Uterine secretions increase the motility of sperms and thus probably shorten their duration of life. Tubal extracts have no demonstrated effect on sperm, whereas the findings on the effects of ovarian or follicular extracts seem to be contradictory. Peritoneal and cerebrospinal fluids have been shown to have a harmful effect on sperm.

Oxygen is necessary for normal sperm activity, but spermatozoa can survive being deprived of this element for varying periods. Various drugs such as strychnine, chloral hydrate, and tutocain have been tested in a limited way for their action on spermatozoa, and in proper dilutions they seem to have a stimulating effect.

As indicated above, spermatozoa cannot survive a rise in temperature much above normal body temperatures, and they are killed by slow freezing. Instantaneous freezing without the attendant destruction of the colloidal nature of the protoplasm seems to have no deleterious effect on spermatozoa of some species and might prove very useful in preserving sperms from valuable breeding animals. Shaffner at Michigan and Purdue has demonstrated the ability of fowl spermatozoa to cause fertilization after being frozen for short periods. Sunlight stimulates

[1] See Allen, E., Danforth, C. H., and Doisy, E. A., "Sex and Internal Secretions," 2d ed., pp. 681–685, The Williams & Wilkins Company, Baltimore, 1939. (Paper by Carl G. Hartman.)

the spermatozoa and thus shortens their life, but the evidence for the effect of X rays is contradictory.

Motility is, of course, generally necessary to assist in the transport of spermatozoa to the site of the egg for successful fertilization. Motility itself, however, is not a sure indication of fertilizing power. Experimental work has revealed the fact that spermatozoa lose their fertilizing power before they lose the power of motility.

Sperms are formed through two rapid cell divisions of the spermatogonia which line the seminiferous tubules. They are not particularly active as they pass along the tube giving them egress. Their passage is slow, and it is thought that they continue to mature during passage. This ripening is marked by the slow backward displacement of the Retzius protoplasmic droplet, which moves backward from the head toward the tail as the spermatozoa travel. This journey through the tubules, rete, epididymis, and vas deferens takes several days. The spermatozoa are stored in the tail of the epididymis, in the ampulla of the vas deferens when present, and in the head of the epididymis to some extent.

Spermatozoa are produced in tremendous numbers, and, although the supply could theoretically become exhausted, this seldom happens in practice. It has been estimated that the average man secretes about 1000 billion sperm during his lifetime. Hammond reports a rabbit serving 39 times in 8 hours without loss of fertility; and Kirillow and Morosow report a bull ejaculating 24 times in 27 hours with a high sperm count at the last service. Males should not of course be overworked, but if this happens they generally recover very quickly.

Spermatozoa.—In every normal ejaculation, there are billions of spermatozoa. From the time of puberty until senility, they are continually being secreted in the tubules of the testicles of the higher mammals and stored ready to be ejaculated into the female genital tract at copulation. A normal spermatozoon consists of a head, a body, and a tail portion. The head is usually rounded or pear-shaped and contains the chromosomes. These, together with the chromosomes of the ovum, determine the potential characteristics of the new individual. The head of the sperm is composed chiefly of nuclear material that is covered by a thin layer of cytoplasm. A caplike structure called the *acrosome* is frequently observed on the anterior surface of the head. The body region contains the centrosome, which functions in cell division. There is considerable variation in the size and shape of spermatozoa of different species of animals, though the basic plan in all of them is similar. At fertilization the spermatozoon pierces the ovum, and the tail, which has already performed its function in propelling the spermatozoon to the ovum, is quickly lost or absorbed.

As found in the testicles or epididymi, the spermatozoa are not very active. It is the remaining portion of the semen, the secretion of the accessory glands, as well as the normal secretions of the vagina and uterus of the female that activate them.

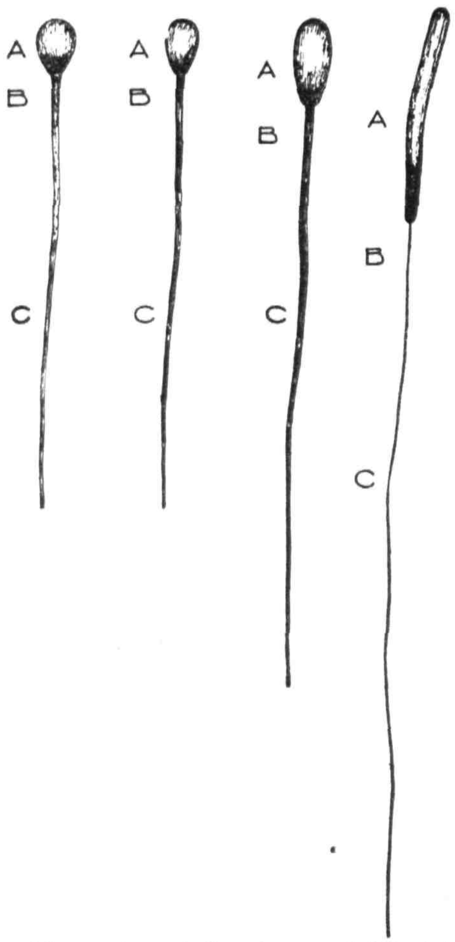

FIG. 37.—Spermatozoa of human, horse, bull, and rooster, left to right. (*From Anderson, Ky. Bull.* 239.)

The spermatozoa have a dual function: *viz,* to provide the offspring with the paternal set of chromosomes and to initiate cell division on the part of the egg. In some of the lower organisms, this latter function can be supplied by means of a hot needle, causing the egg to develop parthenogenetically and exhibiting, therefore, maternal characteristics only.

Spermatozoa were first observed by Ham, a student of Leeuwenhoek, in 1677, but their significance in inheritance was not realized at that time. About the middle of the eighteenth century, Spallanzani, by filtering semen, showed that the spermatozoa were the essential factor in reproduction, for the filtrate proved to be impotent. Shortly after Kölliker had shown that the spermatozoa arise from the testis, Barry, in 1843, observed the conjugation of the sperm and egg in the rabbit.

The size of spermatozoa varies considerably in various animals, but in any case they are extremely minute, that of the human being $\frac{1}{300}$ in. in length. Savage and his coworkers state the head length of spermatozoa of the bull to be 9.7 μ and those of the stallion 6.16 μ. Phillips reports the head length of ram spermatozoa to be 8.15 μ. After puberty, spermatozoa are being continually produced in the testicles of the higher mammals at varying rates, and those not ejaculated are resorbed.

Abnormal spermatozoan forms are usually observed in small numbers in the ejaculate of highly fertile males. Large numbers of abnormal sperms, however, are quite generally associated with lowered fertility or sterility. Methods of collecting and evaluating semen will be discussed in a later chapter.

Length of Life of Spermatozoa in Female Genital Tract.—Experiments have demonstrated that spermatozoa live but a short time in the female genital tract in the higher animals, probably 36 to 48 hours in most cases. Live sperms have been recovered in woman 7 days post coitum, but this is exceptional. It has been reported that spermatozoa deposited in the female bat in the fall are capable of fertilizing eggs several months later, and, although this may be the normal procedure in this species, some workers feel that bats usually mate again in the spring. In fowl, fertilization has been known to occur up to 32 days following insemination in the hen, 10 days in the duck, and 8 days in the ringdove. Among insects, the queen bee has been known to lay fertile eggs for 7 years following the last insemination. Long periods of this sort are also known among fish and turtles.

In spite of the above facts, we must realize that the store of energy in a tiny sperm is not overlarge and that, when the seminal fluid is deposited in the female genital tract of the higher animals, the spermatozoa are immediately plunged into violent activity. It would seem reasonable to expect, therefore, that their tenure of life would be brief. This undoubtedly is generally the case, and we are safe in assuming that we can reckon their functional activity in hours rather than days. Because it has been shown also that the egg is generally capable of fertilization for a period of but a few hours following ovulation, it becomes obvious that the breeder's task is to see to it that viable sperm are deposited in the female genital tract at about the same time that the egg is released from the

ovary. A further consideration, with which the last two sections of this book will deal, is that of having the proper hereditary materials in these eggs and sperms so that a worth-while offspring may result.

Rate of Travel of Spermatozoa.—The older conceptions regarding the rate at which spermatozoa traveled up the female genital tract were that it was a matter of several hours before they reached the distal end of the ovarian tubes. These ideas have had to undergo considerable revision in the light of later findings. When placed in proper media, mammalian spermatozoa have been clocked at speeds of from 1 to 4 or 5 mm. per minute with the average at about 3 mm. per minute. Many workers have found that the sperms reach the junction of the uterus and tube in periods as small as 10 minutes. Whitney (1927) recovered sperm in the ovarian bursa 18 minutes after coitus, Lewis and Wright (1935) within 15 minutes in the mare, and Phillips and Andrews within 30 minutes in the ewe.

This leads to the question as to whether or not the penis of the male actually penetrates the cervix and deposits the sperm directly in the uterus. This would seem to be impossible for anatomical reasons in many species, although in others it may be possible. If not deposited directly in the uterus, the semen is at least in most species deposited at the very mouth of the cervix. There have been many claims that the cervix, under the stimulation of estrus and copulation, operates with a peristaltic or sucking action, which forces the semen quickly into the uterus. The evidence on this point at the moment is somewhat contradictory, and no definite answer to the question is now possible.

It has long been contended that there exists a chemotactic attraction between the egg and sperm, but the most recent experimental work gives no clear indication that such an attraction is an actuality.

Transport of Spermatozoa through the Uterine Tubes.—

The cilia of the oviducts of all vertebrates beat for the most part downward towards the exterior, as has long been known. Parker, however, discovered in the turtle and the pigeon a discrete band of cilia which beat toward the ovary. These latter function to carry sperms upward into the body cavity.

No such continuous band of cilia causing adovarian currents has been found in mammals—the ciliary current is all abovarian, but the principle that sperms are carried as if they were passive elements applies nevertheless, the conclusion reached by Parker (1931), whom we follow in his interpretation of the observed facts.

If one studies the intact tube of the rabbit in vivo by strong transmitted light a new picture presents itself and a new interpretation of the function of the tubal trabeculae comes to light (cf. Henle, Göttingen Nachrichten, 1862). The cavity of the tube is seen to be broken up by its folds and muscles into a system of longitudinal compartments. Next to their mucosal walls abovarian currents are observed, in the centers adovarian counter currents. Eddies are thus formed

which are calculated to carry sperms as well as inert particles like carbon in all directions. These compartments being temporary, due to the muscular activity of the tube there is continuous exchange of contents between adjacent compartments, in consequence of which sperms are gradually working along the tube. The old observation that first a few, then more and more sperms reach the ampulla (Hammond, 1934) is quite in agreement with this "compartment" theory of sperm ascent. Carmine particles injected into the middle of the tube reach either end after a period of time.

Phillips and Andrews make the interesting observation that rat sperms, injected into the vagina of the ewe along with ram sperms, lag behind the latter in their "race" upward. This phenomenon needs explanation. Under the Parker theory both sets of sperms should proceed at an equal rate if their motility is no factor, that is, if they are transported as inert particles.[1]

Summary.—The male's part in reproduction consists of the production of spermatozoa and their deposition in the female genital tract. The first of these purposes is accomplished by means of the testes, the second by means of the accessory glands and organs. The same basic anatomical and physiological plan is found in all the higher animals. Spermatozoa are formed at the far end of the tube, and their passage along the tube reminds one of an assembly line, the sperms maturing as they progress and being joined by various sorts of secretions as they move along, the final combined ejaculate being the semen. Successful breeding practice involves the understanding of the whole process and the factors affecting any of its phases for good or ill in order that males may be kept in vigorous breeding health and that the breeder may appreciate how much his future success depends on the content of the tiny seminiferous tubules located in the testes of his male animals.

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CHAPTER V

THE FEMALE'S PART IN REPRODUCTION

In all the higher species of animals, fertilization and embryonic development take place within the female genital tract. Understanding the structure and physiological functions of these organs is a prime requisite for anyone who would succeed in the art of livestock breeding. Enormous financial losses are incurred annually by breeders because of the difficulty so often experienced of getting females to conceive and, although it is unjust to lay all the blame at the door of the females, their share of the total fault is no doubt considerable. "Knowledge is power" and an understanding of the processes involved in fertilization, gestation, parturition, and lactation would often enable a breeder to avoid the fatalities that so often threaten individuals before as well as after birth.

Ovaries.—Mammalian females possess two ovaries, homologous to the testicles of the male; and, like the latter, the ovaries arise from the intermediate portion of the mesodermal somites and have a double function: (1) the production of ova or eggs and (2) the secretion of hormones. In other words, the ovary performs an ovogenetic as well as an endocrine function. The ovaries are generally spoken of as the primary organs of reproduction in the female because of their ovogenetic function and because they are the source of the female sex hormones. The development and functional activity of the remaining portions of the female genitalia are dependent upon the second function of the ovary, *viz.*, its endocrine function. An internal secretion of the ovary stimulates the growth of the uterus and vagina and other hormonal secretions from the corpus luteum, which appears cyclically in the ovary, sensitizes the uterine wall for the reception of the fertilized egg, maintains the pregnancy, and assists at parturition. These secretions together with others from the placenta stimulate mammary development and lactation following parturition. In some species ovogenesis is practically continuous after puberty. In others it occurs once, twice, or a few times a year.

In the higher animals, these glands are situated in the abdominal or the pelvic cavity suspended in the broad ligament. Their position varies somewhat in different species and in different individuals. They are attached to the broad ligament on one side at the so-called "hilum." From this point the tissues of the broad ligament spread out and pass through the ovary, forming the ovarian stroma, made up of fibrous con-

nective tissue. Toward the surface, the stroma becomes interspersed with glandular tissue that forms the ovarian cortex. Surrounding the ovary is a rather dense layer of fibrous tissue called the *tunica albuginea* and outside this is found a modified peritoneum, the inner portion of which consists of a single layer of cuboidal cells and which is known as the *germinal epithelium.* It is from the latter that the ova arise.

In the mare, the ovaries are somewhat bean-shaped and 2 to 4 in. in the longest diameter; in the cow, 1 to 1½ in.; in the ewe ½ to 1 in.; and in the sow somewhat larger than in the ewe and more irregular, owing to the many protuberances of the follicles and corpora lutea which give them a shape somewhat like a bunch of grapes.

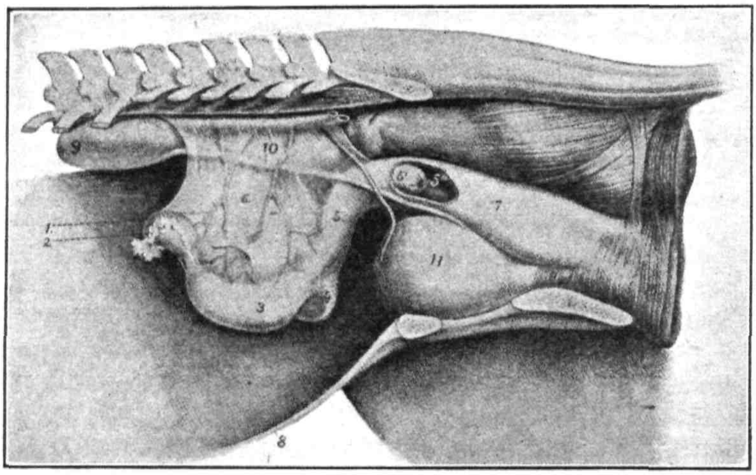

Fig. 38.—The generative organs of the mare. 1, left ovary; 2, Fallopian tube; 3, left horn of uterus; 4, right horn of uterus; 5, body of uterus; 6, broad ligament; 7, vagina; 8, abdominal wall; 9, left kidney; 10, left ureter; 11, urinary bladder. (*From Leisering, Atlas of the Anatomy of Domesticated Animals.*)

The ovary consists of glandular, connective, and nerve tissues, blood and lymph vessels, and many thousands of follicles in various stages of development. The last, which arise from the germinal epithelium, are found all through the stroma of the ovary, and each contains an immature ovum that, when matured, is liberated and may be fertilized by a spermatozoon and produce a new individual. It has been estimated that there are upward of 75,000 follicles in the ovaries of a heifer calf at birth. Only a very small percentage of these follicles would ever ripen, even though the cow was never bred and came in heat regularly once in 3 weeks for 10 to 15 years. In this case, the ovaries would gradually become fibrous because of the deposition of the small plugs of connective tissue, the end result of the absorption of corpora lutea. The newer concept of a continual production of new ova from the germinal epithelium, similar

to spermatogenesis in the male, would involve the production of even greater numbers of follicles, most of which atrophy and are absorbed before reaching maturity. This continuous process of ovogenesis from the layer of germinal epithelium is comparable to the continuous process of spermatogenesis in the male. It is now claimed to exist in the mouse, rat, guinea pig, dog, cat, monkey, and mare and is probably the general method of egg production in all the mammals. In either case, nature has attempted to ensure the perpetuation of the race by providing a superabundance of both spermatozoa and ova.

The ovarian, or Graafian, follicle at first consists of the egg cell surrounded by a single layer of epithelial cells. Surrounding this is a specialized layer of ovarian connective-tissue stroma known as the *theca*. As growth proceeds, the epithelial cells multiply and push out away from the ovum forming an antrum, which becomes filled with a yellowish, alkaline, albuminous fluid, the liquor folliculi. The ovum itself remains on a small hillock of epithelial cells, the cumulus oöphorus. There is some variation in the size of the ova of different mammalian species, but they measure on the average about 0.13 mm. This is greatly in excess of the size of the sperm, which has little or no cytoplasm. The egg, on the other hand, has a nucleus with its contained chromosomes of about the same size as the head of the sperm, and in addition it has a considerable amount of stored cytoplasm, or yolk, in which the nucleus is suspended. This makes the egg several thousand times the size of the sperm, but the dam is actually no more important than the sire from an hereditary standpoint, for both egg and sperm have a nucleus of equal size in which are found an identical number of chromosomes (with the possible exception of sex chromosomes in some species). The stored yolk of the egg is presumably designed to provide energy for the developing zygote for the first few days following fertilization and until the zygote can pass down the ovarian tubes into the uterus and find another source of energy and materials for growth. The developing follicle passes toward the periphery of the ovary, finally protruding from the ovary to the extent of half its size or more preparatory to being liberated. This maturing of the ovum in the ovary occurs at more or less regular intervals in farm animals and is usually accompanied or preceded by estrus, or heat.

This cyclic development of a mature ovum begins at puberty, under the stimulation of an anterior pituitary hormone. As noted in the previous chapter, the development of ova from Pflügers egg cords begins early in embryonic life. These embryonic follicles, however, and those from birth to puberty are atretic. Puberty marks the time when a follicle succeeds in reaching full maturity with the attendant maturing of the egg and reduction of the number of chromosomes to one-half. It is now thought that waves of follicles start developing cyclically throughout the

reproductive life of the female, one or a few of them reaching full maturity, the others being resorbed preceding the next wave.

In the production of a functional ovum, or egg, the primordial egg cell in the follicle goes through two rapid cell divisions. Previous to the first cell division, synapsis occurs; and the net result of the first division,

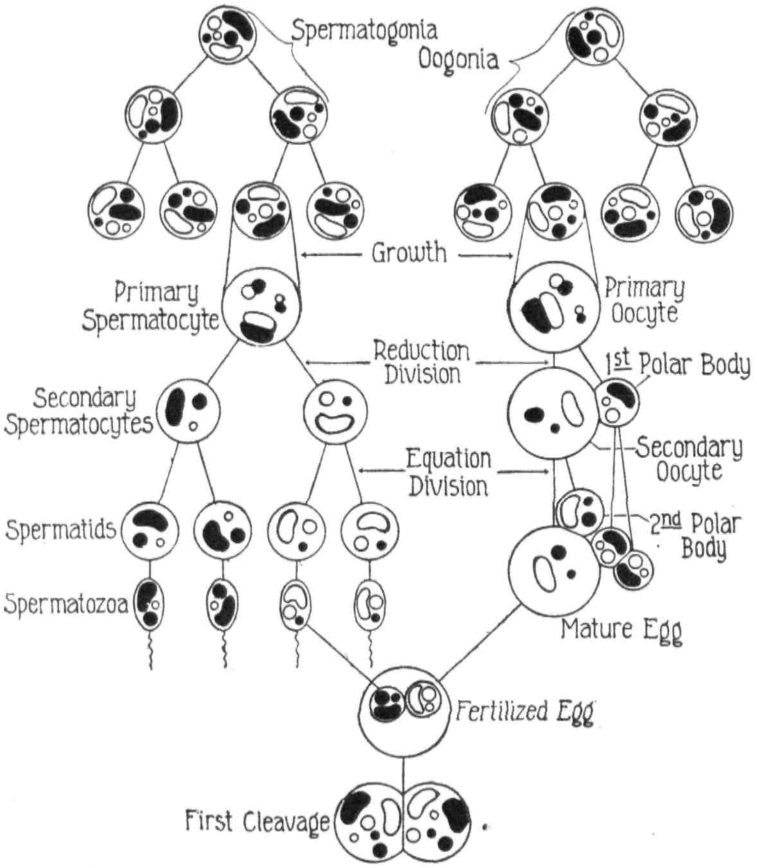

FIG. 39.—Diagram of maturation or meiosis of germ cells in animals. The process begins with the third row of cells. Maternal chromosomes white, paternal black. All chromosomes *in the fertilized egg received from the mature egg are thereafter maternal,* and those received from the spermatozoon are thereafter paternal, regardless of what they were in the mature germ cells. (*After Shull.*)

which takes place in the ovary in mammals, except perhaps in the bitch, is a reduction in the number of chromosomes to one-half the number characteristic of the species and the very unequal division of the cytoplasm. This is known as the *heterotypic division* and is followed by a second homotypic cell division in which the chromosome number is not

further reduced. The one mature ovum now passes into the peritoneal cavity of the broad ligament and then into the uterine tube.

Starting with a primary germ cell, or oöcyte, in the ovary, the reduction division, including synapsis, and the formation of tetrads is the same as found in the male, except that in the female, instead of two secondary spermatocytes, there are formed one secondary oöcyte and one nonfunctional polar body, each of which, however, has received one-half the chromatin material and contains one-half the normal number of chromosomes. In effect, the nucleus, rather than the whole cell, divides. The polar body differs from the secondary oöcyte in having received none of the yolk or cytoplasm. These two, the secondary oöcyte and the polar body, then divide, the oöcyte giving rise to one ovum or egg and one more polar body. The first polar body may give rise to two polar bodies. The ovum is the female gamete that is capable of being fertilized by a spermatozoon. The three polar bodies are nonfunctional and are later absorbed. So, whereas in the male there are produced four functional spermatozoa from each primary spermatocyte, from the primary oöcyte of the female in the higher forms there arise but one functional ovum and two or three nonfunctional polar bodies.

The purpose of the reduction division in the formation of germ cells, in both the male and the female, is to keep the number of chromosomes for the species constant. When an ovum with one-half the normal number of chromosomes is fertilized by a spermatozoon, also with one-half the normal number of chromosomes, the summation of the two halves restores the normal number of chromosomes in the zygote that is to produce the new individual. No doubt, some cases of sterility in hybrids are due to the fact that the two species that were crossed had different characteristic numbers of chromosomes, and, although fertilization and subsequent development are possible, it is nevertheless impossible for the hybrids to produce functional spermatozoa or ova, because the normal pairing of chromosomes and subsequent cell mechanism is interfered with.

So far as known, the distribution of chromosomes in germinal mitosis is at random. The solid chromosomes in Fig. 75 represent those contributed by the male, those in outline by the female. Following synapsis and disjunction, one member of each pair will proceed to one pole and be found in one cell, the other member of each pair will go to the other pole and be found in the other cell. The fact that one member of a certain pair goes to one cell has no influence on the distribution of any of the other chromosome pairs; in other words, the distribution is independent, or random, it being understood that one or the other member of each pair must normally go to each daughter cell. Figure 75 represents all the possible combinations of the eight chromosomes of Drosophila.

As will be pointed out later, random distribution is one of the most potent causes of variation.

We meet here again the all-important fact that any of the higher organisms passes on to each of its offspring a sample half of its entire inheritance, one member of each pair of its chromosomes. Our whole purpose in making a study of breeding principles will be to learn how our animals may be made more pure in their genetic content of desirable genes, so that it will make no particular difference which member of each pair of chromosomes any offspring may chance to get.

Factors Affecting Ovogenesis.—As is true of spermatogenesis in the male, we find a great many physiological and environmental factors that affect ovogenesis. Because endocrine influences in reproduction and lactation are to be treated in the next chapter, we will here confine ourselves to environmental considerations.

The previous chapter showed that both light and temperature had important effects on the seasonal manifestations of spermatogenesis. These environmental factors also play an important part in ovogenesis. Animals below the Primates show very distinct breeding cycles, and it is only at these times that the female will accept service by the male. In the invertebrates, eggs are laid only at certain specific times during the year. This is also true of the lower vertebrates, fish, amphibia, and reptiles. Birds likewise mate only at specific seasons, although selection, feeding, and housing have to some extent obliterated this feature in the domestic fowl. Mares, ewes, and, to some extent, sows usually have their breeding seasons restricted to certain times of the year, whereas in cattle, especially dairy cattle, seasonal manifestations of breeding activity have been practically eliminated. The above actions are undoubtedly controlled by environmental factors, particularly temperature, and length and intensity of daylight, as well as nutritional and physiological factors.

Nutritional factors undoubtedly play an important part in sexual manifestations in females. Underfeeding reduces the size of the ovaries and, especially, their power to develop mature follicles. The harmful results of underfeeding in the female are even more marked than they are in the male. Ovogenesis is affected earlier than spermatogenesis of the male, and there is an accompanying atrophy of the uterus. Inanition has been used experimentally to produce abortion, fetal resorption, stillbirth or the production of small weak offspring in the guinea pig and rat, although within limits fetal growth will go on at the expense of maternal tissues.

Likewise, a low protein intake may result in abortion or failure to conceive, and the inclusion of more calcium and phosphorus in the ration of cattle has been followed by a lowered abortion rate. Iron and copper are also known to be essential for normal reproductive functioning. For

ovogenesis to occur normally a sufficient amount of energy, proteins, minerals, and vitamins must be supplied, and, although the mother's system may supply them for a while from her own stored reserves, this supply is relatively quickly exhausted.

Other than its effect on general health, the lack of vitamin A seems to have no particular influence on the ovary or on ovogenesis, at least in rodents. Its absence from the diet does, however, affect the uterine epithelium, which undoubtedly would interfere with successful implantation, and exaggerated cornification of the vaginal wall also results from a deficiency of vitamin A. The effect of the lack of vitamin A from the diet seems, therefore, to have a less deleterious effect on the ovary and ovogenesis than we noted in the preceding chapter on the testes and spermatogenesis, but it is essential to other body functions.

The vitamin B complex has been shown to be necessary for normal functioning of the ovaries of birds. The ovaries are reduced somewhat in size, and the follicles do not develop. In mammals a deficiency of vitamin B leads to impaired growth, a retardation of sexual growth or permanent anoestrum in the immature, and an abrupt cessation of estrus in the mature, with an accompanying atrophy of the ovaries and uterus. Experimental results seem to indicate that all the above results may be secondary to the general loss of appetite and consequent lowered general health which follows deprivation of vitamin B, at least in mammals.

Vitamin C, a normal cytoplasmic constituent of all living cells, acts as a stimulant in cellular metabolism and respiration. It would seem logical to expect therefore that it might have a direct effect on ovogenesis, but it has not yet been demonstrated that a lack of vitamin C will of itself cause degenerative changes in the ovary. The recent work of Phillips *et al.* at Wisconsin, as noted in the previous chapter, has opened up an interesting field for experimentation with shy breeding females.

Vitamin D, formed through the action of ultraviolet light on ergosterol and therefore closely related chemically to the follicular hormone, the male sex hormone, and the carcinogenic hydrocarbons, has not been demonstrated to have any direct effect on ovogenesis and related phenomena. The practical impossibility of increasing the vitamin supply of a growing fetus through feeding the mother and also of greatly increasing the content of vitamin D in milk through feeding practices has led to a greater appreciation of the necessity of supplying adequate amounts directly to young, growing animals.

Vitamin E is absolutely essential for the normal development of a fetus and the prevention of abortion or fetal resorption in the rat. The ovaries and uterus do not seem to be manifestly affected through lack of vitamin E, nor are the processes of estrus, ovulation, and implantation. Extensive changes do result, however, in both the fetus and fetal mem-

branes and placenta, the latter being especially affected, resulting in asphyxia and starvation. Abortion has been successfully treated in many species by the administration of wheat-germ oil or other sources of vitamin E.

In female rats deprived of the essential fatty acids, there usually occurs an irregularity, and sometimes a complete cessation, of oestrus. The experimental data so far presented have not satisfactorily eliminated growth retardation as a significant factor in inhibition of the oestrous rhythm. Rats successfully mated manifest varying degrees of fetal resorption, prolonged gestation, disturbances of the birth mechanism, birth of weak and undersized offspring, and impaired lactation; a sequence of events seemingly identical to those observed by Mason (1935) in the A-deficient rat. Equally similar are the atrophic changes in the uterine mucosa and maternal decidua and in the corpora lutea, as extensively described by Maeder (1937). It would appear that there is much yet to be learned regarding the role of fats, and of fat-soluble vitamins, in placental function. Restoration of the essential fatty acids to the diet readily restores oestrous irregularities and, after variable periods of time, permits normal reproductive function in most animals; but, in some instances, the latter capacity is permanently lost. Likewise, lactation is improved but never highly successful. (Evans, Lepovsky and Murphy, 1934a).[1]

The cyclic nature of ovogenesis has already been referred to. Pregnancy does not necessarily stop this procedure, and some animals will accept service while pregnant. Large follicles have been reported in the mare and cow early in gestation and perhaps exist in all other species. The waves of follicles probably subside gradually as gestation proceeds, although cases of superfetation, or the carrying of young of different ages within the uterus, have been reported, some eventuating in normal births at normal term for each embryo. Following parturition, normal ovogenesis is again renewed at varying times in different species: in the mare from 4 to 11 days; cow varying times averaging about 40 to 50 days; in the sow 3 to 6 days; ewes after a period of several months.

Secondary Sexual Characters.—Like the male, the female also exhibits characteristics peculiarly associated with her sex and referable, as are the development and functional activities of the accessories, to hormones secreted by the ovaries. This is the second main function of the ovaries.

These characteristics are to be found largely in the general body form and are generally not as striking as those found in the male. The typical male form is heavy or well-developed anteriorly, less well-developed posteriorly. In the female, the exact opposite prevails. The mammalian female develops a wider pelvis and a general feminine type expressed in

[1] ALLEN, E., DANFORTH, C. H., and DOISY, E. A. "Sex and Internal Secretions," 2d ed., p. 1196, The Williams & Wilkins Company, Baltimore, 1939. (Paper by Karl E. Mason.)

finer bone and more refined features than the male. The deposition of fat differs from that in the male, the voice is higher pitched, and she differs also in psychological traits.

There are several types of female sex hormones; the estrogens, produced in the ovary and having to do with the production of the female secondary sexual characters and the growth of the uterus, vagina, and mammary glands; the progestins, secreted by the corpus luteum; and the placental hormones. The latter two will be treated later in this chapter and the estrogens in the following chapter. The estrogens are found widely in nature, in the Graafian follicle, corpus luteum, and placenta, in the blood and urine of both women and men, in eggs, cow's milk, liver, and bile, and even in yeast, some vegetables, grains, and flowers.

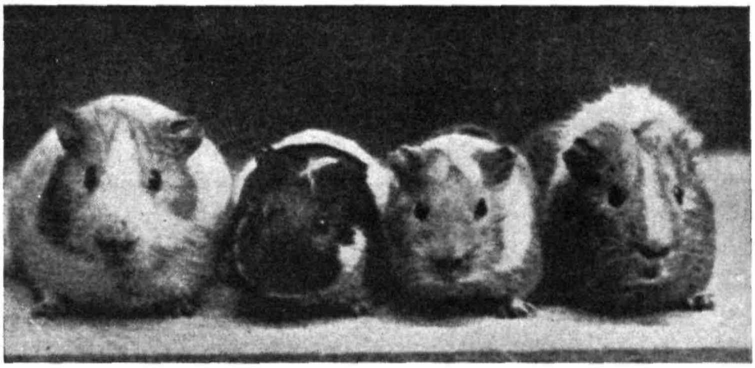

FIG. 40.—Feminization of guinea-pig. (*From Steinach.*) Reading from left to right, the animals are arranged in the following order: Normal male, two feminized brothers, castrated brother. (*F. H. A. Marshall, Physiology of Reproduction, Longmans, Green & Co.*)

These extracts may not be identical with the follicular hormone, but they are known to have similar effects.

The various correlations and reciprocal relation between the ovarian hormones and those secreted by the other ductless glands will be treated in the next chapter.

Castration.—This operation in the female is more generally called *spaying*. It has not been practiced to nearly so great an extent as its counterpart in the male. The reasons for this are undoubtedly two: first, the operation is more difficult, necessitating an abdominal rather than a scrotal incision as in the male; and, second, the results are not generally so striking. There is not so marked a general body change, the quality of the carcass is not so greatly improved, fattening propensities are not so greatly enhanced, and there are less noticeable psychic changes.

Following castration, the female loses some of her "femininity" and "quality." She may fatten a little more rapidly, etc., and her pelvis will not be quite so wide, but to most livestock breeders the gains are

not considered to be worth the bother and risks involved. In the fowl, removal of the ovary generally leads to the adoption of male plumage at the next molt, but it has no effect on comb or voice, which are conditioned only by the presence of the male sex hormone.

It has been often demonstrated that castration of either sex followed by successful transplantations of gonadal material from the opposite sex leads to the assumption of secondary sexual characters coincident to the transplanted material. The secondary sexual characters are thus proved positively to be due to gonadal secretions, just as for long ages the same thing had been "proved" by noticing that such characters did not appear in animals which had been subjected to castration.

This concludes our consideration of the primary organs of reproduction in the female, the ovaries, although we shall have to return to them when we further consider ovulation, fertilization, embryology, and the formation and functions of the corpus luteum. In the meanwhile, we will consider the various female accessory organs of reproduction.

Fallopian Tubes.—The Fallopian tubes, ovarian tubes, or oviducts, act as excretory ducts of the ovaries, conveying ova from the ovaries to the uterus. They are not, however, in direct continuity with the glands but rather partly in continuity with and partly attached to them, both ovaries and oviducts being suspended in a fold of the broad ligament, the mesosalpinx. Their anterior ends open into the peritoneal cavity, and posteriorly they join the horns of the uterus or the uterus proper.

Their analogues in the male are the vasa deferentia. The Fallopian tubes consist of an inner mucosa and outside this a circular and a longitudinal muscularis and an external serous coat. They are firm to the touch and have a diameter of about 0.1 in. in the cow. The fimbriated, or funnel-shaped, end of the oviduct nearest the ovary is called the *infundibulum*. The middle portion consists of the dilated ampulla and the constricted isthmus, whereas the portion entering the horn of the uterus is called the *intramural* portion. The mucosa of the oviduct is thrown up into folds and is richly supplied with lymphatics and thin-walled blood vessels, indicating a secretory. activity. The epithelial lining of the oviduct is often ciliated, and the ciliary motion is chiefly toward the uterus. Spermatozoa that are desposited in the vagina or uterus at copulation pass up these tubes to their upper end, where fertilization usually takes place as soon as the ovum is liberated.

Experimental removal of one ovary and tying off of the opposite oviduct has been followed by pregnancy. In some way, in other words, the egg produced by one ovary moved across the peritoneal cavity to the other oviduct and on down to the uterus. Dukes suggests that this may be due to the action of the cilia in the infundibulum setting up a current in the peritoneal fluid, the cilia beating toward the uterus.

The fertilized ovum or zygote passes down one of these tubes in from 3 to 4 days in domestic animals to find lodgment in a horn or in the body of the uterus. For this purpose, aid is perhaps derived in some species from the cilia or microscopic fingerlike projections from each of the cells that line the inside of the oviduct and by a waving motion tending to push the ovum downward. In other species, however, cilia are lacking in the oviducts, so that the downward passage of the zygote is probably here referable to the peristaltic action of the musculature of the tubes, even though this is made up of small waves rather than one continuous wave (see page 123). Like the rest of the female genital tract, the oviducts and their glands become more active at estrus. Fallopian tubes, the lumina of which are smaller than the lead in a pencil and greatly convoluted, act somewhat in the nature of a seal, thus preventing anything harmful passing down into the pregnant uterus. It can readily be seen, too, that, if infection of any sort once found lodgment here, it would be exceedingly difficult to combat or to eliminate. The most usual type of sterilization operation in woman consists of the severing and tying off of the oviducts so that sperm are not able to come into contact with the egg.

Uterus and Horns.—The oviducts in the higher animals terminate in the horns of the uterus, and the two horns terminate in the body of the uterus. It is here, of course, that the embryo undergoes its prenatal development. In the human, the horns of the uterus are practically lacking. In the mare the body of the uterus is nearly equal in length to that of the horns, whereas in the cow, ewe, and sow the body is short and the horns long. The horns, or cornua, are long and straight in the dog and cat, long and coiled or folded in the sow, and long and curved, somewhat like a ram's horns, in the cow, ewe, and goat. The horns and uterus proper are lined with a highly vascularized mucosa bounded by two layers of muscle fibers, the inner circular and the outer longitudinal layers. This muscular structure provides the uterus with the degree of elasticity necessary for pregnancy and also provides the means for the final expulsion of the fœtus at time of parturition.

The external covering of the horns and uterus is the serosa. The mucosa of the uterus is highly vascularized and contains many glands and lymph spaces. During sexually mature life it is undergoing rhythmic changes due to the heat periods, the inner surface being renewed periodically preparatory to the rupture of eggs from ovaries. The glands increase in size and activity at this time also. The fertilized egg descends the oviduct and finds lodgment in or on the uterine mucosa. Parts of the inner uterine wall become modified forming the maternal part of the placenta by means of which the embryo receives its materials for growth. This may be a circular or disklike area, as in woman and the

mare, a zone or band, as in the bitch or cat, or rows of cotyledons or caruncles, as in the cow and ewe.

Cervix.—The uterus terminates posteriorly in the cervix, or neck of the womb. This is a very thick-walled portion of the genital tract. It is lined with simple epithelial cells that secrete copious amounts of mucus into the small canal passing through the cervix. The thick muscular walls are thrown into many folds that expand at time of parturition to allow passage of the fetus and then retract in a few days to their contracted state. The cervix forms an effective seal at the posterior end of the uterus.

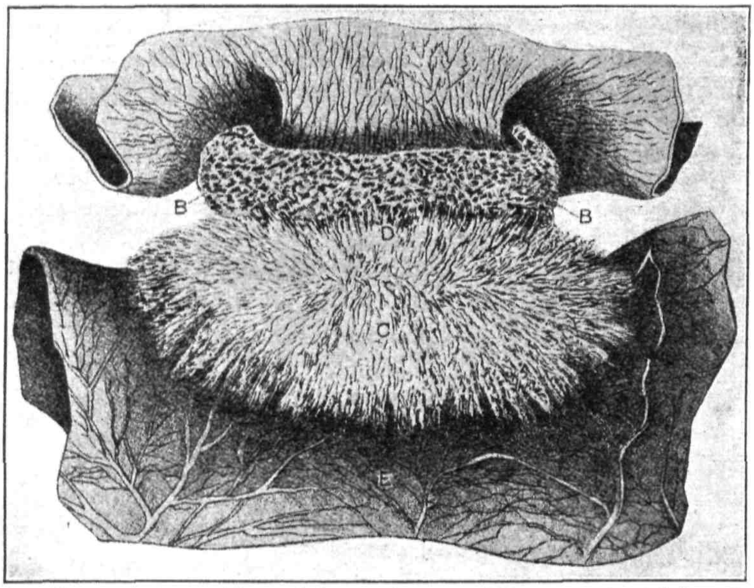

FIG. 41.—Pregnant uterus with cotyledons. *A*, uterus; *BB*, maternal cotyledon; *D*, fetal cotyledon. (*From U.S. Department of Agriculture, Diseases of Cattle.*)

In the mare, the cervix is 2 to 3 in. long and 1½ in. in diameter. The cervical canal is straight and never fully closed in the nonpregnant state. In the cow it is about 4 in. long with a wall 1 in. or more in thickness and is always tightly contracted except at parturition. The canal through the cow's cervix is spiral, folds of tissue being thrown back on each other making it difficult to dilate or to insert an instrument of any sort. In the ewe, the cervix is about 1½ in. in length, and the lumen is tightly contracted and difficult of entrance as in the cow, whereas in the sow it is about 4 in. long, partly occluded by rounded prominences on its interior and has no intravaginal projection as found in the mare, cow, and ewe.

The character of the mucus secreted by the cervix varies considerably at different times of the reproduction cycle. During estrus, the mucus is thin and watery, the cervix also somewhat relaxed. Both these conditions render passage of the semen into the uterus more easy. Following heat, the mucus thickens and remains in this condition until the next heat period. Following the onset of pregnancy the cervical

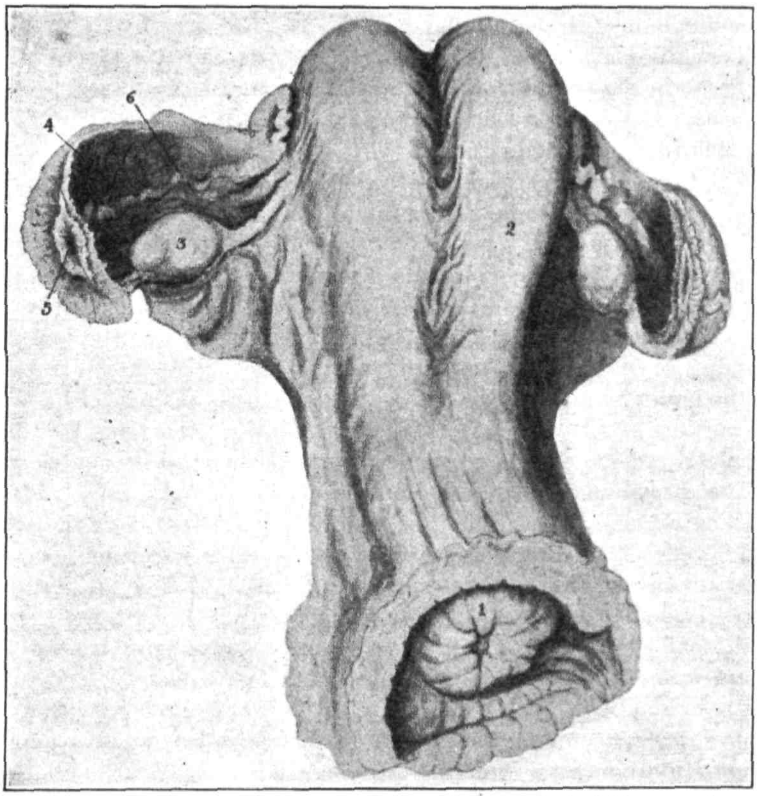

FIG. 42.—Portion of generative organs of cow. 1, os uteri; 2, right cornu; 3, ovary; 4, ovarian ventricle; 5, fimbriated end of oviduct; 6, oviduct. *(From Williams, Diseases of the Genital Organs of Domestic Animals.)*

mucus becomes very thick, forming a more or less solid and permanent plug that seals the cervix and thus protects the developing embryo. Disturbance of this plug is often followed by abortion, but the reaction here is quite variable among both individuals and species. Owing to its structure, especially in the cow, pathological conditions in the cervix are particularly hard to treat.

Vagina.—From the cervix posteriorly to the urogenital sinus or vestibule, the female genital tract is termed the *vagina*. In farm animals

it lies horizontally below the rectum and above the bladder. This portion of the tract is relatively simple both in structure and function. It consists anatomically of the usual three layers of tissue: mucosa, muscularis, and serosa. The epithelial lining of the vagina is very responsive to cyclic sexual changes, and these changes have been intensively studied and correlated with the phenomena of estrus, ovulation, etc. in laboratory animals and in woman. During estrus the cellular epithelial lining of the vagina proliferates, becomes highly stratified. During interestrus it is less active and consists of fewer layers of cells. In the mare the vagina is about 6 to 8 in. long; in the cow 8 to 10 in.; in the ewe 3 to 4 in.; in the sow 4 to 5 in. The vagina generally becomes longer during the pregnant state.

The function of the vagina is twofold: (1) to receive the intromittent organ of the male at copulation and probably in most cases the ejaculate also and (2) to provide a passage for the fully developed fetus at term.

Vulva and Clitoris.—The female genital tract terminates posteriorly in the vulva or external orifice. With the onset of heat, or estrus, these structures become congested and enlarged, particularly in the sow, somewhat less so in the cow, the mare, and the ewe. The clitoris, the small erectile organ homologous to the penis in the male, is situated just inside the portion of the vulva farthest removed from the anus. Sufficient stimulation of the clitoris results in a sexual orgasm in the female.

The Breeding Season.—Many species of animals have a definite breeding season that in general is definitely correlated with the seasons of the year. The breeding season under natural conditions occurs as far in advance of the onset of the growing season as the gestation period covers; *i.e.*, the periodicity of the breeding season is conditioned by the nutritional needs of the offspring. Reproduction among the lower animal forms is very directly influenced by temperatures, food supply, length of daylight period, and general environmental conditions. In many species of animals the sexual instinct is called into play only by definite environmental stimuli. Although not so marked in the higher forms of life, these influences, nevertheless, do play an important part. During the breeding season, both the male and female generative organs are brought into a high state of functional activity. During the rest of the year, these organs are more or less quiescent and very much reduced in size. The oviduct of the common fowl when not laying is 6 to 7 in. long and about ⅛ in. wide, whereas during the laying period it is nearly 2 ft. in length and nearly ½ in. in width.

Domestication of farm animals has resulted in an almost complete obliteration of seasonal breeding manifestations. Cows and sows will breed at any season of the year, the ewes of certain breeds will breed in the late spring and summer as well as in the fall months, and mares

in late winter, all spring, or in the fall. The testicles of the males of these species are functional continually from puberty till senescence, although at varying rates according to age, season, plane of nutrition, etc. In man it is a well-established fact that most births in the United States occur in February (conception in May or June), most conceptions in Sweden occur in June, and those of Greece in April. The exact physiological mechanism that regulates the manifestations which have been discussed under the heading of "The Breeding Season" is not fully known. That they are responsive to both internal and external stimuli cannot be questioned. Hours of daylight, food supply, temperatures, endocrine activities, etc., are known to have an influence on the onset and duration of breeding activities.

The Sexual Cycle.—We have seen in the previous section that there is a certain periodicity in the breeding season of most mammals. That portion of the breeding season during which the uterus is comparatively anemic, the generative organs relatively inactive, and in which the female will not countenance any sexual advance on the part of the male is known as *anestrus*. This is followed by a period of preparation during which the uterus becomes highly vascularized, its glands enlarge and become more active in secretion, the epithelial lining of the vagina thickens, the vulva may begin to swell, and there may follow more or less discharge of blood from the vulva. The breeder calls this the period when the animal is *coming in heat*. Technically, it is known as the *proestrus* and is a building up period. It results from the action of an anterior hypophyseal hormone acting upon the ovary to cause a wave of follicles to start development and growth toward maturity. As the follicles enlarge, there is an increased production of their hormone, estrin, in the follicular fluid; and this hormone stimulates the cells of the tubes, uterus, vagina, and vulva to greater activity.

This leads to the period of sexual excitement in the female and she now welcomes and accepts the attention of the male. This is known as the period of *estrus*. It is normally accompanied by the ripening of one or more follicles in the ovary, further preparation on the part of the uterus to receive and nourish the egg, the relaxation of the cervix, and the liquefying of its mucus, a marked swelling of the vulva in the sow (less in the ewe, cow, and mare), the characteristic whinnying and friendliness toward the stallion in mares, bellowing and riding of other animals in cattle, loss of appetite and general nervousness in sows and ewes. Most females urinate frequently at this time. The extrusion of blood from the uterus through the vagina and vulva at estrus is usually entirely lacking in farm animals, though present in the bitch and sometimes in the cow. This is sometimes erroneously spoken of as *menstruation*, a term applicable to the Primates only.

Estrus lasts 6 to 30 hours in the cow, 1 to 3 days in the ewe, 1 to 5 days in the sow, and 2 to 11 days in the mare. The length of the estrual cycle varies with individuals. It is influenced by the state of nutrition, age, weather, general health, etc. As far as known, no drug (excepting hormones) is known to have any specific influence on the length of the cycle, and the same can be said for the psychological effect of the proximity of the male or of the service by the male. A disturbance of the normal rhythm of estrus may ensue from pregnancy, cystic condition of the ovaries, persistence of corpora lutea, disease, or abnormal nutritional conditions. Hammond has shown a positive correlation in cattle between the length of the estrual cycle and the duration of the ensuing estrus. Removal of the corpus luteum generally results in a rather rapid onset of a shortened estrus. As will be pointed out later, estrus is a most critical period, because it is only in this restricted time that fertilization can occur, because the ova very quickly lose their functional powers.

Estrus is thought to be brought to a close by the rupture of the Graafian follicle, or ovulation. In species like the rabbit, cat, and ferret, which do not ovulate spontaneously but require the sexual act to bring about ovulation, estrus persists until the follicles degenerate. In farm animals, estrus follows quickly on the heels of proestrus. In the human female, on the contrary, the ovum is not liberated from the ovary until about 2 weeks after the initial onset of menstruation. In the bitch, also, ovulation is delayed until 7 to 12 days after proestrus. If, in farm animals that are bred at estrus, fertilization of the ovum or ova takes place, this is followed by the periods of gestation, parturition, lactation, and finally by another period of anestrus or another estrus.

The period following estrus is known as *metestrus*. Immediately following ovulation, the corpus luteum begins to form in the ovary at the site of the rupture. This develops rapidly, within 3 to 5 days, generally, and the stage of the estrual cycle when the corpus luteum is active as an endocrine gland is commonly spoken of as the *luteal phase*.

The corpus luteum develops, largely from the granulosa and theca cells that surrounded the follicle before its rupture from the ovary. These cells proliferate rapidly and become more or less loaded with the lipochrome lutein. This is very marked in the cow, which, therefore, has a very yellow-colored corpus luteum. The functions of the corpus luteum will be discussed later in this chapter.

The built-up wall of the vagina becomes invaded with leucocytes during late metestrus, and this recent growth begins to desquamate at late metestrus, and the vaginal wall returns to its resting stage, consisting of a reduced number of epithelial cells. The inner layer of the uterus is maintained at a high level of activity during the luteal phase.

Metestrus is, therefore, a period of further preparation for pregnancy, but it is mostly a period of marking time, waiting to see whether fertilization has or has not occurred.

Diestrus is the period following metestrus. Its length, course, and termination depend both on whether or not the ruptured egg has been fertilized and also, of course, on the species involved.

If fertilization has taken place, the corpus luteum persists, generally through pregnancy. Its hormones sensitize the uterine wall for implantation, as well as preserve the pregnant state and make preparations for parturition. A condition known as *pseudopregnancy* follows the failure of fertilization in some species. In the bitch, for example, if breeding has failed or not been allowed, the corpus luteum persists for the next 63 days, and the bitch at the proper time often goes through all the motions of getting ready to have a litter of puppies. In the rabbit, if fertilization fails following copulation with a male, the doe has a pseudopregnant period lasting about one-half as long as the normal gestation period of 32 days.

In other species the failure of fertilization leads in a few days to the beginning of the absorption of the corpus luteum and the return of the uterus, tubes, and vagina to their resting state.

This is followed by either a short or a long period of rest from sexual activities. If it is a short period and the animal returns to proestrus within a few days or weeks and continues this process more or less indefinitely, it is said to be a *polyestrus* animal; if for only a relatively short time, a *seasonally polyestrus* animal; whereas, if the animal goes into a rather long rest period and consequently has only one or two heat periods a year, it is said to be *monestrus*.

The following summarizes the events of the sexual cycle.

THE SEXUAL CYCLE

Name of sexual phase	General activity	Type of cycle
Anestrus	Quiescent	Either
Proestrus	Beginning	Either
Estrus	At its height	Either
Metestrus	Preparation for implantation; marking time	Either
Diestrus		
Egg fertilized	Active embryonic development	Either
Egg unfertilized	Receding or pseudopregnant state	Either
Followed by either		
Proestrus	Beginning	Polyestrus
or		
Anestrus	Quiescent	Monestrus

Ovulation.—Ovulation is the freeing of the ovum by the rupture of the follicle in the ovary. As indicated in the previous section, this takes place in animals during the estrus or heat period, except those, of course, which do not ovulate spontaneously. Many theories have been proposed to account for the freeing of the egg from its follicle; *e.g.*, pressure from within the follicle, pressure induced from the blood supply of the ovary, muscular contractions in the ovary or the follicle, and the action of proteolytic enzymes in the liquor folliculi.

It has now been abundantly demonstrated that the ripening of a Graafian follicle is due to the action of anterior pituitary hormones. This discovery has already been made use of with some success in inducing mares, which normally have a long and uncertain heat period, to ovulate at specific times and, in conjunction with artificial insemination, has led to high rates of conception. It has also been shown experimentally that if one ovary is removed the remaining one does double duty; *i.e.*, a given amount of pituitary hormone calls out a characteristic quantitative reaction from what ovarian tissue is present. In a reverse fashion the secretion from the corpus luteum, progestin, retards ovulation, which makes superfetation unusual and of very rare occurrence.

In the nonspontaneously ovulating rabbit, as well as in some other animals, many things have been found, experimentally, that cause ovulation. Among these might be mentioned electric stimulation of the hypophysis and mechanical stimulation of the vagina or cervix, whereas in many lower animal forms various neural and environmental stimuli are known to induce ovulation.

The evidence available, however, clearly points to the secretion of the anterior pituitary as the causative agent in ovulation in the higher mammals. It has been further demonstrated, however, that anterior pituitary hormone is not necessary for the initial stages of ovogenesis. The completed growth and rupture of the mature follicle, however, does depend upon the presence of pituitary hormones. The follicle grows slowly for most of its life and will reach a certain stage without pituitary hormone. For its last rapid spurt in growth, however, and for the rupture of the follicle with the consequent loosening of the egg into the infundibulum, anterior pituitary hormones are essential. In the rabbit, follicles grow to maturity at estrus, but, if the doe is not bred, these follicles do not rupture but atrophy, and a new set develops.

It has been shown that the size of the Graafian follicle bears some relation to the size of the animal species concerned, but this is not true of the egg itself. During the final rapid stages of follicular development, the chromosomes in the egg are reduced to one-half the somatic number by the budding off of a polar body containing half the chromosomes

but little or no cytoplasm, the thickening of the liquor folliculi, and the breaking up of the discus proligerus or cumulus oöphorus.

Time of Ovulation.—In the past 12 years, many workers have actually observed the occurrence of ovulation, motion pictures have been made of it, and the fact of a sudden change in electric potential between the cervix and the ventral body wall at ovulation has been established for several species, including woman. As observed, the process is a gradual one and not in any sense explosive or cataclysmic. The ripened follicle pushes against the wall of the ovary, one or several areas of the follicle become avascularized, thin, and more or less transparent until finally the wall ruptures at one point, and the stringy follicular fluid with the contained egg oozes through into the peritoneal cavity or the infundibulum.

The time of ovulation is of very great practical importance to livestock breeders. Considerable experimental work has been done on all classes of farm livestock to ascertain just when ovulation does occur. The following table gives the present known facts.

TABLE 11.—ESTRUS AND OVULATION IN FARM MAMMALS

	Range of estrus	Average length of estrus	Time of ovulation
Mare......	2–11 days	6 days	24–48 hours before end of estrus
Cow......	6–30 hours	19 hours	Within 24 hours after end of estrus
Ewe......	1– 3 days	35 hours	At end of estrus
Sow......	1– 5 days	3 days	Near end of estrus

From the above table it is evident that cows and ewes should be bred toward the end of their heat periods, the sow on the second day of heat, and the mare on the fourth and sixth days of heat. The fact that mares are so variable in the preovulatory duration helps to explain the fact that their rate of conception is below that of the other farm animals.

The question as to whether the ovaries share equally and alternately in the production of viable eggs cannot at this time be given a definite answer. The meager data available indicate that in the mare and sow the left ovary is more active than the right with the reverse of this indicated in the cow and ewe. If one ovary is removed or becomes nonfunctional, the other simply does double duty.

Vitality of Ova.—It has long been known empirically that animals must be mated during estrus if viable young are to be produced. This indicates that the ova remain functional for but a short time following ovulation. In 1911, Lewis at Oklahoma force-bred 13 sows a total of 34 times about a day following the cessation of estrus. From these matings but one pregnancy resulted. Experimental work with many

small laboratory animals has proved that the egg remains viable and capable of fertilization and normal embryonic development for only a very few hours following its rupture from the follicle. These facts have a very important application in the field of animal breeding.

Fertilization.—A hormone from the anterior pituitary causes a number of follicles to begin their final rapid growth and maturing processes. Eventually one or several (depending on individuality and species) follicles become fully mature, a process which includes the reduction in the number of chromosomes to the haploid number through the budding off of a polar body containing one member of each pair of chromosomes. The follicle finally ruptures, and the egg is liberated during estrus. At this time the female will accept service by the male and billions of spermatozoa are introduced into the distal end of the vagina, into the cervix, or possibly in some species directly into the uterus. In the course of a very few hours masses of spermatozoa have been transported through the uterus and tubes to the upper end of the latter.

These sperms, with the reduced number of chromosomes, await the appearance of the egg, also with the reduced number of chromosomes. The ovum drops or is swept into the infundibulum and one spermatozoa immediately pierces it. This stimulates the ovum to throw off the second polar body. An immediate change in the wall of the ovum prevents additional sperms from entering. Immediately following, the tail of the sperm is dropped or discarded, the male and the female pronuclei approach each other within the ovum, the centrosome brought in by the middle piece of the sperm divides, a portion moving to each pole of the cell, and the paternal and maternal chromosomes finally become arranged in the equatorial plane. This process is known as *fertilization* and is completed with the fusion of the male and female pronuclei and the arrangement of the chromosomes in the equatorial plane. It is probable that fertilization is completed within a few hours after service by a normal male on a female in estrus.

In recent years mammalian ova, especially from the rabbit, have been secured and have been fertilized in test tubes, the process having been observed. They can then be inserted into the uterus of a properly stimulated female, and embryonic development will proceed normally to term in the foster mother. Pincus (1939) has recently caused development of the rabbit ovum without stimulation by the sperm. This is the long-sought mammalian parthenogenesis and occurred, according to Dr. Pincus, because of an early restoration of the diploid number of chromosomes through nuclear diversion without cell division.

In the multiparous animals it is seldom that all the eggs liberated are fertilized and implanted, the loss in the sow having been determined to average 20 to 30 per cent and to run as high as 50 per cent. Multiple

ovulations in the cow and mare are also known to be more numerous than multiple births, which in these species is a good thing. It is better, too, from a practical standpoint, for a sow to have 10 or 12 good-sized vigorous pigs than 20 or 25 small, weak ones, the large majority of which generally die very early.

The fertilized egg, or zygote, immediately begins (1) to grow by cell division and (2) to descend the Fallopian tube into a horn or the uterus proper. The egg is huge compared with other body cells because of its stored yolk. Its early segmentation does not involve an increase in size but rather an increase in cell numbers and a consequent reduction in the size of the cells to that characteristic of other body cells of the species. Cell divisions proceed at first at the rate of one or two a day. The passage down the tube is probably effected by both ciliary and muscular activities of the oviduct and takes from 3 to 4 days. The oviduct also produces a secretion that may help to nourish the egg in its passage downward. Normally the mass of cells reaches a horn or the uterus proper (though ovarian, abdominal, and tubal pregnancies occur now and then) and becomes attached to the uterine mucosa where embryonic development proceeds.

Attachment generally occurs in the larger farm animals in the horn of the uterus corresponding to the ovary that contains the corpus luteum, but many cases of migration and implantation in the opposite horn have been recorded. In multiparous animals like the sow, implantations occur at more or less regular intervals throughout the two horns, regardless of the fact that most of the eggs may have been produced by one ovary or, as demonstrated by Warwick, after removal of one ovary. The exact mechanism regulating the site of implantation is at present unknown.

Corpus Luteum.—The corpus luteum (yellow body)[1] is an intermittent or periodic gland of internal secretion that is formed within the follicle after ovulation. Upon rupture of the follicle and liberation of the ovum, there ensues a rapid vascularization of the granulosa and theca cells that surrounded the follicle and sometimes an escape of blood from the theca into the follicular cavity. The cavity closes over and with the retained blood clot is known as the *corpus hemorrhagicum*, which is the earliest stage in the development of the corpus luteum. The connective-tissue cells of the theca folliculi, which have arisen from the ovarian stroma surrounding the follicles, gradually grow in and partially fill the follicular cavity, the blood clot gradually undergoing absorption. The granulosa cells of the undischarged follicle hypertrophy. The rapidly multiplying cells of the theca, under stimulation of the luteinizing hormone from the anterior pituitary, absorb yellow

[1] The corpus luteum is yellow in the cow but is pink in the sow and ewe.

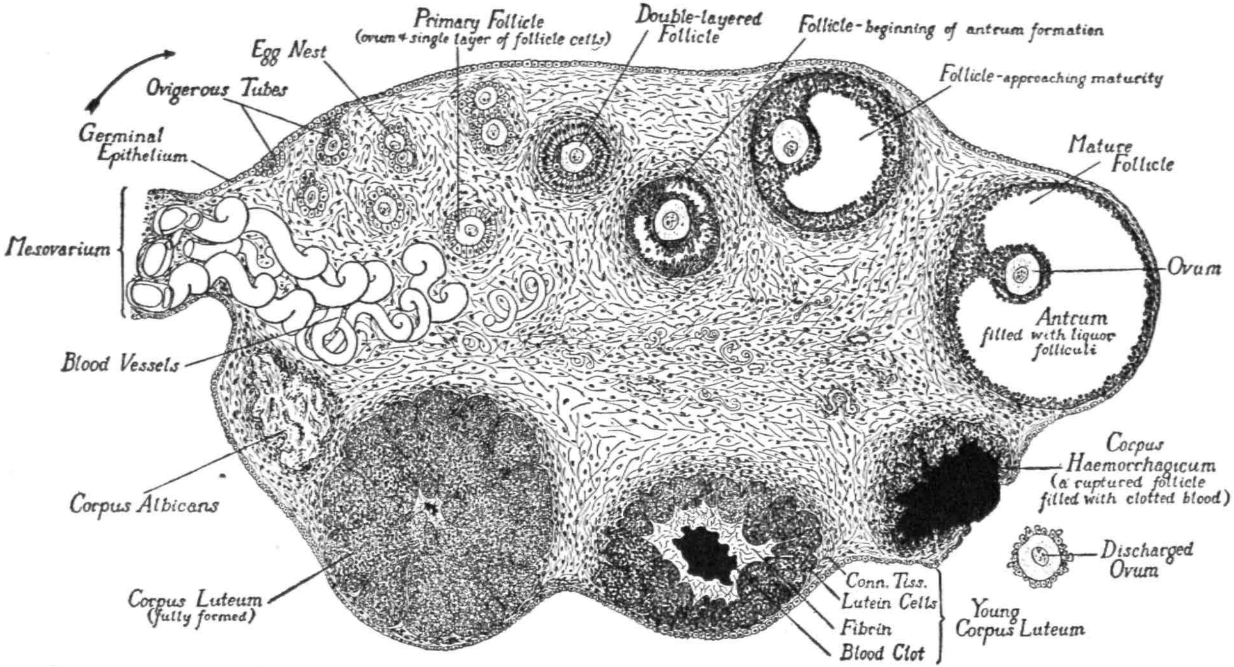

Fig. 43.—Schematic diagram of mammalian ovary showing the sequence of events in the origin, growth, and rupture of the ovarian (Graafian) follicle, and the formation and retrogression of the corpus luteum. Follow clockwise around the ovary starting at the arrow. (*From Patten, Embryology of the Pig, 2d ed., P. Blakiston's Son & Co.*)

lipoid pigment and fat droplets, which gives to the corpus luteum its characteristic yellow color, which varies, however, in different species. Blood vessels are carried in with the ingrowing tissue from the theca, making the corpus luteum a highly vascularized gland. The corpus luteum grows quickly, soon filling the follicular space and usually protruding from the ovary, its later growth being due to enlargement of the cells rather than to cell multiplication.

If the animal conceives, the corpus luteum continues to enlarge until about the middle of the gestation period. It then often begins to shrink in size and to decrease in secretory activity until it finally degenerates and becomes the corpus albicans. In some species it is not wholly absorbed until a considerable time after parturition. If conception does not occur, the corpus luteum does not grow so large, and absorption begins before the onset of the next estrual period; in fact, this absorption may be looked upon as a necessary prerequisite to the next estrus.

The Graafian follicle at first secretes estrogen, but its cells, after forming the corpus luteum, begin the secretion of the luteal hormones typical of the corpus luteum, *viz.*, progesterone and later relaxin. This change is brought about through the action of the luteinizing hormone of the anterior pituitary, although a reduced amount of estrogen probably continues to be secreted by the corpus luteum.

The functions of the corpora lutea hormones are as follows: (1) progestational changes in the endometrium of the uterus that are necessary to sensitize the uterine wall before implantation of the morula can take place as well as the early development of the placenta, (2) the regulation of the estrus cycle by preventing estrus and ovulation until the corpus luteum reaches a certain stage of atrophy, (3) the maintenance of pregnancy, (4) the relaxation of the pelvis at parturition, and (5) some participation, it seems, in the development of the mammary gland.

The amount of luteal tissue necessary to lead to successful implantation has been determined for some species. It has been shown in many species that removal of the corpus luteum shortens the sexual cycle by quickly inducing the next heat period, which in the cow generally follows within 48 hours.

In many species removal of the corpus luteum during pregnancy results in the absorption of the fetus or an abortion within 1 to 10 or 12 days. If performed very soon after fertilization, abortion or absorption is practically certain to follow. Some species can evidently safely dispense with the corpus luteum much earlier than others, and in those cases it is thought that the placenta may then take over some of the functions of the missing corpus luteum, for the relaxation of the pelvic muscles occurs normally as does the development of the mammary glands.

A new set of corpora lutea is formed in the mare during the first third of pregnancy, replacing those that have involuted.

The whole of the reproductive process appears, therefore, to be under endocrine control, the main control residing in the pituitary that secretes a gonad-stimulating hormone. At puberty, secretions stimulate the testicles and ovaries to the production of viable germ cells, and the development of the gonads in turn stimulates the growth of the accessory organs of reproduction and the development of the secondary sexual characters. The follicular hormone, estrin, sensitizes the uterus for successful implantation and early development of the embryo. The corpus luteum secretion, progesterone, also functions in continuing the development of the uterus, inhibiting ovulation during pregnancy, and gradually relaxing the pubic region so that the fetus can be expelled. The final atrophy of the corpus luteum following parturition again allows the pituitary secretion to function in stimulating the ovaries to the ripening of more follicles and to ovulation.

Placenta.—The placenta consists of two parts: (1) the maternal placenta, which is of maternal origin, and (2) the fetal placenta, which is of fetal origin. The fertilized egg, or zygote, obtains its nourishment at first from its own stored yolk and perhaps also from its investing envelopes, the zona pellucida and the corona radiata. Next it subsists on materials secreted by the uterine glands, absorbed directly at first and obtained later by means of the yolk sac. Finally, it becomes embedded in or attached to the uterine wall, the placenta is developed through which food materials pass inward to the embryo, and waste materials pass outward from it by means of the placental blood vessels.

Following segmentation, which produces a solid mass of cells (morula stage), a central cavity is formed within the mass of cells (blastula stage). Then there ensues an invagination (gastrula stage), and the embryo proper develops from the invaginated cells. The portion remaining outside is called the *trophoblast.* At first each blastomere is nourished independently, but, following invagination, the trophoblast is concerned wholly with the nourishment of the embryo that is to be elaborated. The fusing of the external wall of the allantois, an outpouching from the hind-gut region, with the trophoblast produces the chorion, or afterbirth. The trophoblast is highly vascularized by outgrowths from the blood vessels of the allantois.

In the pig, the blastocysts are spherical for 10 days, but then they rapidly elongate, and by the fourteenth day they together fill the whole length of the uterus. Foldings appear in the trophoblast that fit into folds of the uterus, which increases the area of contact. The trophoblast fits closely to the surface epithelium of the uterus and sends protoplasmic processes between the cells and perhaps down to the underlying layer

of dilated capillaries. Villi do not form in the pig, and the uterine mucosa has no special cotyledonary areas. The placenta of the pig is, therefore, of the contact type (semiplacenta) in contrast to the burrowing type (true placenta), *e.g.*, human. Materials secreted by the uterine glands are absorbed by the trophoblast and transported to the embryo by means of the allantoic blood vessels.

In the mare the lymphatic system of the uterine mucosa is greatly developed, and villi are found in the allantois that fit into tiny crypts of the uterine wall.

In the cow and the ewe there are many special points of attachment between the chorion and the uterine wall. These are called *cotyledons* (buttons), and these species are, therefore, of the polycotyledonary type. There are 70 to 130 cotyledons in the ewe and cow. During pregnancy the cotyledons become spongy, owing to increased vascularization and the enlargement of the lymphatics. Villi containing blood vessels from the allantois grow out from the cotyledonary areas of the trophoblast and become embedded in the tissues of the cotyledons of the uterus. The uterine glands in the intercotyledonary areas as well as the surface epithelium also secrete copiously during pregnancy. This secretion, together with its contained formed constituents (red-blood corpuscles, leucocytes, fat globules, salts, glycogen, etc.) from the blood and lymph systems, is known as *uterine milk*. It seems probable that the exchange of oxygen and carbon dioxide is effected in the cotyledons, where glands are absent and where the maternal and fetal blood systems come into close contact.

The function of the placenta is, of course, the elaboration of the materials necessary for fetal development and the development of a transporting system for conveying food materials to the embryo or fetus as well as waste products away from it. It should be remembered that the mother contributes no blood as such to the embryo. If we think of an island out in midstream as the embryo, then the intervening river and boats plying back and forth might be thought of as the placenta foetalis and the sandy beach of the mainland as the placenta uterina.

The placenta performs an endocrine function as well, and in some species secretes estrogens, progesterone, and gonadotropic hormones.

Embryological Development.—As noted previously, fertilization, or the union of the male and female pronuclei, each with its haploid number of chromosomes, generally occurs in the infundibulum immediately following ovulation. The zygote within the surrounding capsule, or zona pellucida, immediately starts its descent to the uterus. Cell division is inaugurated by the entrance of the sperm and continues during the descent. The time required for the developing zygote to traverse the oviduct probably varies somewhat in different species but consumes a

period ranging from 1 or 2 up to several days. During this time the egg lives and grows upon its own stored nourishment found in the yolk.

Upon entrance into the uterus, the group of cells, probably in the morula stage, takes lodgment upon or in the uterine wall, absorbing nourishment for growth from the uterine secretions until its own developing extraembryonic membranes can set up a connection with the blood vessels of the mother's uterus. It should be understood that the nutrition of the embryo is indirect after the initial stages. The embryo lives first upon the stored nutrients in the yolk of the egg, next upon the uterine secretions, then upon materials carried to the placenta in the

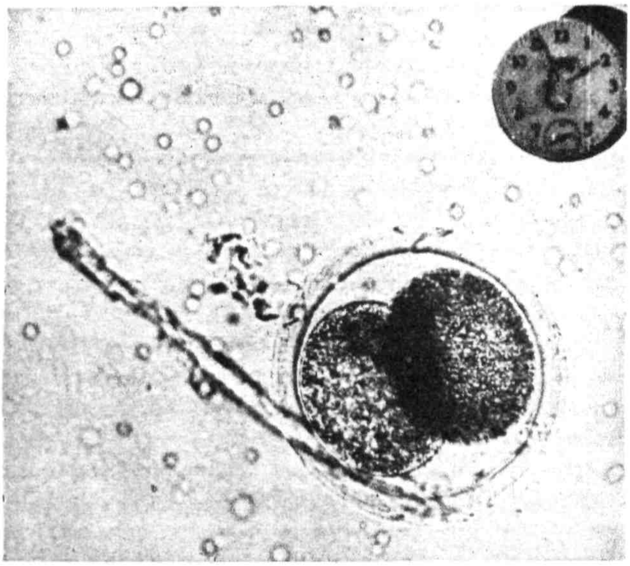

FIG. 44.—Embryonic calf at the two-cell stage. (*Courtesy Bureau of Dairy Industry, U.S. Department of Agriculture,* and *Carnegie Institution of Washington.*)

mother's blood stream, then, in mammals following parturition, upon milk secreted also from the mother's blood, and, finally, upon food that the young has learned how to secure for itself. The embryo never gets any blood as such from its mother. It builds up its own blood, a liquid tissue, in the same manner that it builds up all the other tissues of its body, bone, muscle, nerve, etc., from materials supplied from the mother's blood stream.

The morula, or mulberrylike, stage is succeeded by the blastula, or hollow-sphere, stage, then through an infolding of a portion of the cells the gastrula stage is formed. The outer portion is called the *trophoblast*, the embryo proper being retained inside the blastocoele. A yolk sac is developed dorsally, and, although little yolk is present in the egg of

mammals, the yolk sac functions for about 3 weeks in the cow, sheep, and pig and about 6 weeks in the mare as the medium for supplying nourishment to the embryo. Folds grow out from all sides of the embryo and grow up over it, fusing and enfolding it. This is the amnion, which becomes filled with a watery fluid in which the embryo floats, thus being protected from concussion. From the hind gut there forms an outpouch-

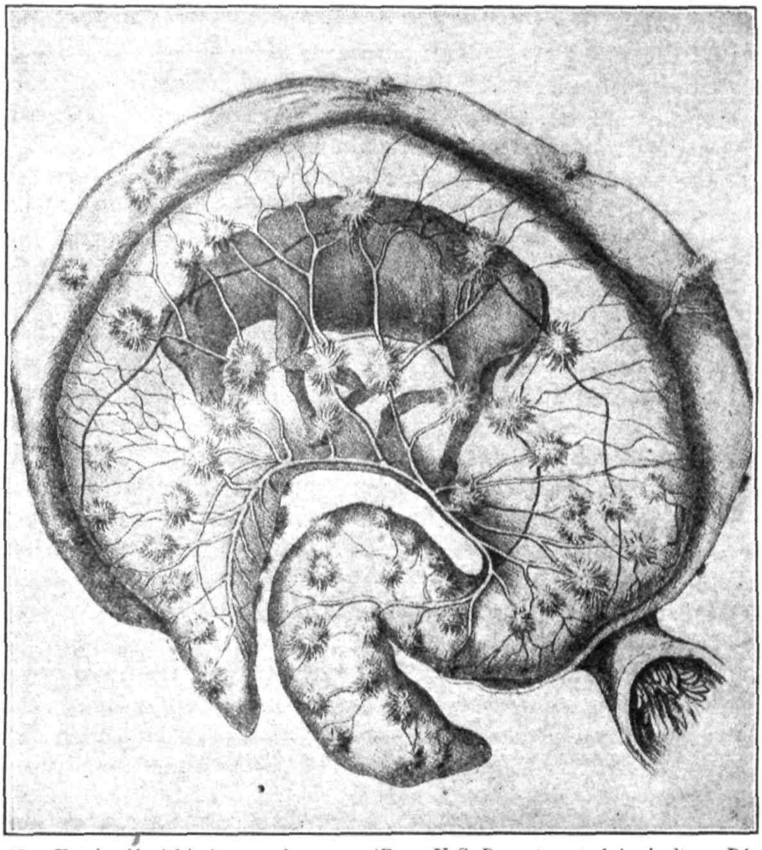

FIG. 45.—Fetal calf within its membranes. (*From U.S. Department of Agriculture, Diseases of Cattle.*)

ing that grows out and enfolds the amnion and its contained embryo. This is the allantois, which is also filled with a watery fluid. Its outer wall fuses with the outer wall of the blastocoele, forming the chorion, or most outward surrounding membrane of the embryo. This fuses more or less securely with the uterine mucosa, forming the placenta. Food materials are carried down into the maternal placenta, there transfuse into the capillaries of the allantoic circulation, and are carried to the

embryo by means of the blood vessels through the umbilical or navel cord. Waste products of the embryo are eliminated by the reverse process. In ruminants, the connection between chorion and uterine mucosa occurs at the cotyledons, or buttons.

Embryonic development is a complicated and marvelous process. The zygote consists of one minute undifferentiated cell. The baby or calf or pig consists literally of billions of cells that have all come from the original zygote. Some have been differentiated into long muscle cells, others into secreting cells (liver, pituitary, etc.), others into bone cells, still others into brain cells. We know little at present concerning the causes of this specialization and of the directing forces involved. It seems peculiar from a genetic standpoint, for all the cells of the body have similar chromosomes. Internal stimuli within the cytoplasm of the cells as well as external stimuli in the different regions (organization centers) of the embryo are no doubt operative in bringing about the transformation from the one undifferentiated cell to its billions of differentiated descendants.

Recapitulation.—An ovum is matured in the ovary, a process usually accompanied by the appearance of estrus or heat; normally the animal is now bred, spermatozoa being deposited usually in the vagina. These spermatozoa at once start their journey toward the ovary, passing up through the cervix, uterus, horn of uterus, and oviduct, or Fallopian tube. Here they await the rupture of the ovum from the ovary. The ovum is carried in the follicular fluid as it oozes from the freshly ruptured follicle into the Fallopian tube, where it is immediately fertilized by one spermatozoon. This successful piercing of the ovum by a spermatozoon causes a change in the wall surrounding the ovum such as to prevent penetration by any more spermatozoa. The fertilized ovum now starts its journey down the oviduct to a horn or the body of the uterus where it becomes attached to or in the wall for its prenatal development. A seal soon forms in the cervical canal in order to protect the embryo. Embryonic development and fetal growth proceed, eventuating finally in parturition, which is followed by lactation.

Chronological Order of Reproductive Physiological Processes.—It is essential for the student and breeder to keep in mind the various physiological processes in the female that are concerned in reproduction. In order of their appearance they are: (1) maturation of the follicle, (2) estrus, (3) copulation, (4) rupture of the follicle, (5) fertilization, (6) formation of corpus luteum, (7) implantation, (8) gestation, (9) parturition, (10) lactation, (11) absorption of the corpus luteum.

Summary.—The female's part in reproduction consists of the secretion of viable ova or eggs in the ovary, their rupture into the infundibulum of the uterine tubes or oviducts, where they are joined by a sperm that

contributes paternal determiners of potentialities and incites the marvelous process of embryonic development which will eventuate in a few weeks or months in a new and unique individual. To use again our analogy of an assembly line, the ova originate at the far end of a big tube; they very quickly (if at all) pick up a sperm and then pass into a roomy cavity where all the marvelous parts are slowly fashioned and fitted together into a completely new individual. As soon as the job is completed, the front door of the uterus, the cervix, which after admitting the sperm was tightly locked to prevent any harmful intrusions, is thrown open and the new individual emerges into a new and strange world. To be successful the breeder must thoroughly understand these processes and the factors affecting any of them for good or ill, in order that breeding operations may be properly timed and conditions made optimum for the eventual bringing into being of superior animals.

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CHAPTER VI

THE ENDOCRINE BASIS OF REPRODUCTION AND LACTATION

by

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We generally think of a huge corporation, a great university, or a modern government as being exceedingly complex organizations, as they are. Likewise the organization, regulation, and coordination of a multicellular living organism is dependent on the interactions of manifold intricate relationships. Just as we might draw up a diagram of the organization of an institution starting at the top with the board of directors or the president and dovetailing each unit into its place in the completed whole, so, since about 1920, scientists have been making discoveries concerning the mechanics of bodily functions and interrelations that enable us now to diagram, in main outline at least, the ultimate causes of bodily organization and function. Cells, tissues, and organs are, by careful experimental procedures, sometimes maintained independently of the organism from which they have been removed, but the well-being of the individual itself is dependent upon the regulation and coordination of all of its individual units.

This function is, to a large extent, performed by the endocrine, or ductless, glands, and no organ, or even a part of an organ, is independent of their influence. A hormone is by definition the secretion of a ductless gland. Hormones are liberated directly into the blood or lymph vessels, usually as rapidly as they are secreted, and are carried in the circulatory system to other regions of the body where they have their effect. They differ from the duct glands, *e.g.*, salivary glands, which pour their secretions onto a free body surface by means of a duct.

Because a complete treatment of the endocrine glands, their anatomy, embryology, physiology, and chemistry, is not within the scope of this text, our discussion will be limited to the generally accepted information on the endocrines as they affect reproduction and lactation.

The Pituitary Gland (Hypophysis Cerebri).—The pituitary gland (often called the *hypophysis*) lies in a bony pocket, the sella turcica, which is located nearly at the geometric center of the skull. It is divided by structure and function into an anterior, an intermediate, and a posterior lobe, each of which is responsible for the production of characteristic hormones. The hypophysis is often considered to be the most important

single gland in the body, for, although it weighs less than 1 g. in the human (about the size of a pea), at least 18 separate hormones have been attributed to it.

The anterior lobe is the most typically glandular portion and secretes the following hormones.

ANTERIOR-LOBE HORMONES

The Growth Hormone.—This substance was first isolated in relatively pure form by Evans in 1922. It stimulates the growth of nearly all organs, with the possible exception of the uterus, and is particularly concerned with the growth of the skeletal and muscular systems. The growth hormone, as would be expected, is secreted most rapidly during infancy and prior to sexual maturity. The male and female sex hormones, produced by the testes and ovaries, respectively, are antagonistic to the growth hormone, and, as the sex hormones are produced in increasingly large amounts at the time of puberty, they are picked up by the blood vascular system and cause the anterior pituitary gland to decrease its production of the growth hormone. This regulatory procedure is responsible for the decreased growth rate that is usually observed at the time of sexual maturity. If excessively large amounts of growth hormone are produced, gigantism may result; if subnormal amounts are secreted, dwarfism may be caused.

The Gonadotropic Hormones.—The discovery of the gonadotropic hormones is usually attributed to Ascheim and Zondek (1927) and Smith (1927) working independently. In 1931, Fevold, Hisaw, and Leonard presented evidence for the fractionation of the gonadotropic hormones into a follicle-stimulating fraction FSH and a luteinizing fraction LH. Much research on the methods of distinguishing, and the separate and combined effects of, FSH and LH has been carried on since 1931, and, from the standpoint of the reproductive physiology of farm animals, their role in the regulation of ovulation and the estrual cycle are of the most importance.

The evidence at hand indicates that at the time of puberty the anterior pituitary gland secretes FSH in sufficiently large amounts to cause the development of one or more mature follicles in the ovary. As the follicle develops, it in turn produces estrogens, the female sex hormones, which cause the female to exhibit heat or estrus. In addition, the estrogens inhibit the production of further FSH by the hypophysis and stimulate the secretion of LH. The luteinizing hormone in turn enters the blood stream and assists in the rupture of the developed follicle and the subsequent luteinization, or development, of the corpus luteum. During the functional life of the corpus luteum, its hormone, progesterone, inhibits the production of FSH by the anterior pituitary, and thus no new follicles

will ordinarily be produced while the corpus luteum is functional. When progesterone is no longer being produced in sufficient amounts to inhibit the production of FSH, new follicles develop, and the rhythm of the estrual cycle is repeated.

If any portion of this regulatory system is upset, abnormalities of reproduction will result. If large amounts of FSH alone are produced and LH is not liberated at the proper time, the follicles that have been developed under the influence of FSH may become persistent or cystic, and nymphomania or constant heat may result. If the corpus luteum fails to regress at the proper time, FSH production will be inhibited and estrus will be prevented. These, and many other abnormalities of the estrual cycle, may be the result of unbalanced endocrine relations.

The effect of FSH and LH on the testis has not been as clear-cut as that on the ovary. Greep, Fevold, and Hisaw (1936) and Greep and Fevold (1937) have shown that in the rat FSH stimulated only the seminiferous tubules in both normal and hypophysectomized males and that LH stimulated only the interstitial cells, or male-hormone-secreting portion, of the gonad. Thus, it would appear that FSH is concerned with spermatogenesis and LH with the production of the sex hormones in the male.

The Thyrotropic Hormone.—The thyrotropic hormone was discovered by the independent efforts of Aron and Loeb in 1929 and is of importance in reproduction and lactation, because both of these processes are partially dependent upon the thyroid gland. If the thyrotropic hormone is produced in increased amounts, the thyroid gland usually increases in size and activity; and, if decreased amounts of this principle are secreted, the thyroid decreases in size and activity.

The Adrenotropic Hormone.—Evans (1933) and Collip (1933) were the first to describe and isolate the adrenotropic hormone. This hormone, which acts upon the adrenal glands, probably consists of two fractions, one which stimulates the adrenal cortex and another which affects the functions of the medulla.

The Lactogenic Hormone.—The lactogenic hormone was discovered by Stricker and Grueter in 1928. After the mammary glands have become fully developed under the influence of hormones, which will be subsequently described, lactation, or the active secretion of milk, is generally believed to be dependent upon the production of the lactogenic hormone by the anterior pituitary gland. Reece and Turner (1937) have shown that the rat pituitary content of the lactogenic hormone increases markedly after parturition and that the prepubertal pituitary of the female is more potent than that of males of the same weight. These same investigators have shown that the pituitaries of beef cattle contain less lactogen than those of dairy cattle and that sexually

mature heifers produce more of this hormone than do steers of the same age.

The Mammogenic Hormones.—Gomez, Turner, Reece, Lewis and Mixner (1937–1940), and others have demonstrated that the growth of the mammary glands is dependent upon substances produced by the anterior pituitary rather than by the direct action of the estrogens and progesterone. These workers have theorized that the mammogenic principles are two in number, a mammogenic-duct growth factor, which is produced by the pituitary under the influence of the estrogens, and a lobule-alveolar fraction, which is produced by the hypophysis following stimulation by the estrogens and progesterone acting in combination. This process will be elaborated upon in a later section.

The Parathyrotropic Hormone.—Because surgical removal or dysfunction of the hypophysis may result in atrophy, hyper-, or hypofunction of the parathyroids, it is believed that a parathyrotropic hormone may be secreted by the anterior pituitary gland. This is of importance in reproduction and lactation only as it may influence the general well-being of the organism.

Other Anterior-lobe Hormones.—At least five other hormones have been ascribed to the anterior pituitary gland. These are of only general interest from the standpoint of the functions being dealt with in this chapter, and they are, briefly: the pancreatropic hormone, which is concerned with the functions of the islands of Langerhans; the nitrogen, carbohydrate, and fat-metabolism hormones, which assist in the regulation of general body metabolism, and possibly an erythropoietic factor, which may be concerned with the production of red-blood cells.

The intermediate and posterior lobes of the hypophysis are closely related, and their secretions will be described together.

INTERMEDIATE- AND POSTERIOR-LOBE HORMONES

Pitocin.—This fraction is usually described as the *oxytocic* substance of the posterior lobe. It stimulates the contractions of the uterus at the time of parturition and is often employed in medical practice to hasten delivery and to assist in the expulsion of the placenta and in the control of hemorrhage. Pitocin does not affect other smooth-muscle systems, and its action during pregnancy is believed to be prevented by the secretion of progesterone.

Pitressin.—This posterior-lobe hormone assists in the regulation of blood pressure, is effective in stimulating peristalsis of the intestinal tract, is concerned with the rate of respiration, and exerts both diuretic and antidiuretic effects.

Metabolic Hormones.—There is evidence to indicate that the posterior lobe may be responsible in part for the regulation of fat, carbohydrate, and water metabolism.

Intermedin and the Melanophore Hormones.—It is believed that the intermediate lobe of the hypophysis secretes at least two substances concerned with pigmentation. Studies of their functions have been limited chiefly to Pisces and amphibia, and the facts are still only partially understood.

THE ENDOCRINE CONTROL AND FUNCTIONS OF THE TESTIS

As previously elaborated, the testis is composed of two types of tissue: the spermatozoa-producing seminiferous tubules and the androgen-producing interstitial cells. Both tissues are intimately concerned in the general endocrine balance of the body, and qualitative and quantitative failures in the secretions of any one of several hormones may result in lowered fertility or sterility.

Pituitary Relations.—Smith (1930) demonstrated that in the rat hypophysectomy was followed by noticeable testicular atrophy within 5 days, and it has been shown that removal of the pituitary results in a testis structure similar to that observed during the nonbreeding season in seasonal breeders. Implantation of anterior pituitary glands in hypophysectomized males has been followed by the restoration of the testes and other portions of the male genitalia to a normal condition, and pituitary implantation into immature males has been followed by precocious spermatogenesis. Fevold, Hisaw, and Leonard (1931) separated the pituitary hormone responsible for these phenomena into a follicle-stimulating and a luteinizing fraction, and it is now believed that FSH is concerned with spermatogenesis and LH with the stimulation of the interstitial cells in the male.

Thyroid Relations.—The best available evidence indicates that the thyroid gland has at least an indirect effect on the testis. The removal of the thyroid before sexual maturity tends to retard the onset of spermatogenesis in the rat, and thyroidectomy in the mature rat tends to decrease sperm production. Zalesky and Wells (1937) found that in the ground squirrel thyroidectomy frequently interfered with normal testicular function. The role of the thyroid in the regulation of the androgens is not clear, but it is known that in the human marked over- or underactivity of the thyroid results in disturbances of the reproductive processes.

Thymus Relations.—The function of the thymus is only partially understood, and its role in reproduction is highly controversial. The fact that the thymus decreases in size after sexual maturity has led to the commonly accepted belief that it is concerned with growth and is antagonistic to reproductive processes. Castration in the immature male does tend to delay involution of the thymus, and the injection of androgens tends to hasten involution. Einhorn and Rowntree (1936–1937) reported that thymectomy in successive generations of rats retarded growth and development. Rowntree and coworkers (1934–1936) reported that when

successive generations of rats were injected with a thymus extract, the later generations matured at a greatly increased rate and that three-day-old rats were indistinguishable from twenty-day-old normal rats. Unfortunately the effects of thymectomy and thymus extracts have been highly variable in other laboratories, and it is impossible to state with any certainty the functions of this gland.

Pineal Relations.—The functions of the pineal are as indefinite as those of the thymus. Anderson and Wolf (1934) reported that pinealectomy had no effect on growth rate or sexual development, whereas Rowntree *et al.* (1935) reported that removal of the pineal retarded growth but accelerated sexual development. The effect of pineal extracts is equally controversial. Rowntree *et al.* (1936) reported that the injection of successive generations of rats with pineal extract retarded growth but accelerated sexual development. As Nelson (1939) points out, it is odd that the removal of a gland and the injection of its extract should have the same effect. Engle and coworkers (1934–1935) found that pineal extracts retarded growth and suppressed the development of the gonads, consequently it must be concluded that the function of the pineal, is at present, obscure.

The Adrogenic Functions of the Testis.—The male hormone is generally believed to be secreted by the interstitial cells of the testis in the form of testosterone. This substance was isolated from bull testes by Laqueur in 1935 and has the empirical formula $C_{19}H_{30}O_2$. Many other androgens have since been isolated or synthesized, but none is as potent as testosterone. Androsterone, a urinary derivative of testosterone and the most abundant natural androgen, is only about one-sixth as effective as testosterone.

As previously elaborated, the androgens are responsible for the development and maintenance of the secondary sexual characters, the accessory genitalia, and sexual desire. The methods of determining the potency of various androgenic preparations are usually based on these primary functions, and such assay methods as the capon comb-growth test, and the prostate, seminal-vesicle, vas deferens, and Cowper's gland cytology tests have been developed. If, for example, it takes ten times as much of preparation *A* as substance *B* to maintain the normal cytological appearance of the prostate cells of a castrate male rat, we know that substance *B* is ten times more potent than substance *A*.

In addition to these easily recognized effects, the testicular hormone is intimately concerned with other endocrine glands. Addison (1917) demonstrated that in the rat the removal of the testis caused the development of a signet-ring type of cell in the anterior pituitary, and Engle (1929) reported that the gonadotropic-hormone content of the castrate pituitary was greater than that of normal males. Injection of androgens

has been observed to hasten the atrophy of the thymus, to prevent the hypertrophy of the adrenals, which usually follows castration in either sex, and to initiate mammary-gland growth in normal and castrate male and female rats. Moore and Price (1930–1937) found that androgens were deleterious to the testes of young growing rats but apparently not injurious to the testes of adult rats. Some workers have reported that the injections of androgens immediately following hypophysectomy prevented testicular involution, but the evidence is not yet convincing on this point.

Various reactions have been observed in the female following the injection of androgens. In some cases the estrual cycles have been inhibited, lactation reduced, menstruation inhibited, and gestation affected.

The literature concerning the role of the sex hormones in the embryonic development of sex is voluminous.[1] In general, it is true that injected androgenic hormones, regardless of the sex of the embryo, tend to develop the male components and to inhibit the development of the female components. Lillie (1916) demonstrated that the freemartin in cattle was the result of an anastomosing of the fetal membranes and blood vessels of twin male and female calf embryos with the resultant modification of the female embryo in the male direction. This modification of the sex of a genetic female is hormonal and results because the male hormones are produced in sufficient amounts in the genetic male twin to cause the development of the rudimentary male components of the female genitalia.

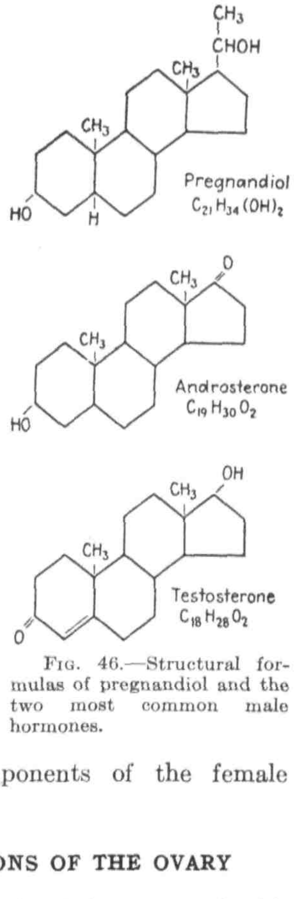

FIG. 46.—Structural formulas of pregnandiol and the two most common male hormones.

THE ENDOCRINE CONTROL AND FUNCTIONS OF THE OVARY

Although the ovary is similar to the testis in that it is concerned with the production of germ cells and sex hormones, the functions of the testis are simple by comparison. The chief duties of the testis are the production of large numbers of viable spermatozoa and their deposition in the

[1] The reader is referred to E. Allen, C. H. Danforth, and E. A. Doisy, "Sex and Internal Secretions," The Williams & Wilkins Company, Baltimore, 1939, for specific information.

female genitalia, whereas the ovary is concerned not only with the production of viable ova but with the nourishment of the developing embryo and with the production of milk after parturition for the continued maintenance of the new individual. The ovarian hormones, either directly or indirectly, are responsible for the development of the vagina and uterus, the nourishment of the fetus, the development of the mammary glands, certain anatomical and physiological processes at the time of parturition, and, perhaps to some extent, the actual secretion of milk.

Pituitary Relations.—Smith (1930) and others have demonstrated that the surgical removal of the pituitary is followed by rapid ovarian atrophy. The primary follicles tend to continue to proliferate, but the larger follicles undergo degeneration. The role of the pituitary in the development of follicles and ovulation has been previously discussed and is dependent upon the interactions of the follicle stimulating, luteinizing, and estrogenic hormones. The maintenance and function of the corpus luteum is also dependent upon the hypophysis, but numerous species differences have been described. Smith (1930) found that rat corpora lutea regressed very slowly after hypophysectomy, whereas in some other species (mice—Selye *et al.* 1933b) the corpora regress at least as rapidly as in normal animals. Pencharz and Long (1931 and 1933) in extensive studies on rats found that removal of the pituitary during the first 4 days of pregnancy prevented implantation, that removal during the seventh to tenth days caused resorption of the fetuses, and that removal on the eleventh to twentieth days resulted in prolonged pregnancy and sometimes in the death of the female and fetuses or both. These effects are at least partially due to disturbances of the pituitary-ovarian relations.

Thyroid Relations.—Under normal conditions the thyroid probably plays a minor part in ovarian activity, but the abnormal function of the thyroid is usually accompanied by atypical ovarian behavior. Hypothyroidism in the human is frequently associated with abnormal menstruation, sterility, and abortion, and hyperthyroidism is sometimes the cause of reproductive disorders.

Thymus and Pineal Relations.—The functions of the thymus and pineal in the female are as little understood as in the male, and the findings previously reported on the male apply to the female as well in most cases.

The Estrogenic Functions of the Ovary.—Although the female sex hormones are widely distributed in nature and have been recovered from such sources as female willow catkins, petroleum, urine, and even the testis, their primary source is in the follicular fluid of the Graafian follicle. Adler, Iscovesco, and others (1912) were among the first to obtain successful ovarian extracts, but it was not until the introduction of the Allen and Doisy vaginal-smear assay technique in 1923 and the finding of

Ascheim and Zondek (1927) that the urine of pregnant women was a plentiful and potent source of the estrogens that rapid advances could be made. Doisy, Veler, and Thayer (1929) were the first to report the isolation of a crystalline estrogen, and Butenandt substantiated their finding by isolating the same crystalline compound a few months later.

Since 1929, many other estrogens have been isolated and other potent compounds have been synthesized. Of the estrogens, estradiol—$C_{18}H_{24}O_2$, estrone—$C_{18}H_{22}O_2$, and estriol—$C_{18}H_{24}(OH)_3$ are most readily obtained. Estradiol is probably produced by the Graafian follicle and is the primary estrogen. Estrone is usually present in large amounts in human-pregnancy urine and is probably a derivative of estradiol. Estriol has been isolated from human urine and the human placenta and is also thought to be a derivative of estradiol.

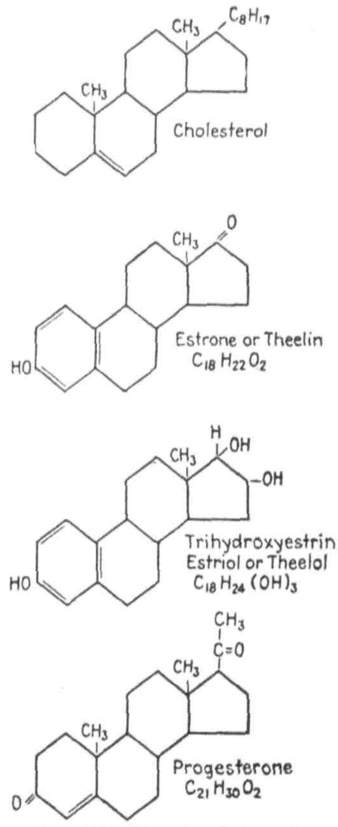

FIG. 47.—Structural formulas of cholesterol, progesterone, and two of the more common estrogens.

The functions ascribed to the estrogens are numerous. Ovariectomy of the adult rat is followed by marked atrophy of the vaginal mucosa, but many new layers of epithelial cells can be produced by injected estrogens within 36 hours. This response is the basis of the Allen and Doisy assay method, the most popular biological technique for determining the potency of the female sex hormone. In immature female rats the injection of estrogens is followed by the rapid development of the vagina and uterus, and it is this same principle that causes the development of the female genitalia at the time of puberty. Sexual receptivity, or estrus, is dependent upon the production of adequate amounts of the estrogens. This phenomenon is first observed at the time of puberty and is the first indication to the livestock breeder that sexual maturity has been reached. Whereas, in the male, sexual desire is not necessarily correlated with the production of spermatozoa, in the female in the case of farm animals the production of ova is accompanied by the development of a Graafian follicle or

follicles containing female sex hormones, which, in turn, cause the onset of estrus and indicate that the proper time for the deposition of spermatozoa in the female genitalia is at hand. The estrogens are also concerned with the rupture of the mature follicle, for it has been theorized that, when the estrogens reach a certain level in the blood, they suppress the production of FSH by the hypophysis and stimulate the secretion of the luteinizing hormone, which assists in ovulation and the subsequent development of the corpus luteum.

In addition to causing the growth and development of the vagina and uterus at the time of and subsequent to puberty, the periodic production of estrogens during the estrual cycle assist in the preparation of the uterus for implantation of the embryo and the fetal development that follows. As previously explained, the estrogens act indirectly, probably through the hypophysis, to reduce the rate of general body growth after puberty and, as will be elaborated upon in subsequent paragraphs, assist in the development of the mammary glands and in the process of parturition.

Although it is a recognized fact that sex is relative rather than absolute, that male and female sex hormones are present in the blood and urine of both sexes, and that stallion urine, for example, is one of the most potent sources of the estrogens, the injection of estrogens into normal males usually has undesirable effects. Among the various reactions observed have been inhibition of testicular growth, testicular degeneration, and abnormal development and function of the male accessory glands. The high incidence of tumors or cancers of the genitalia or mammary glands of women has led to very extensive studies of the carcinogenic properties of the estrogens, and there is little doubt that the female sex hormones are often causative agents.

The Functions of the Corpus Luteum.—Immediately following the rupture of the wall of the Graafian follicle at the time of ovulation, a blood clot forms at the rupture point, and the cells lining the follicular wall increase in size and activity and begin the development of the corpus luteum. These cells, which are now called *luteal cells,* become swollen with stored lipoid material and begin the secretion of their hormone, progesterone. Estrogens may be secreted to some extent by the same cells, especially in fresh or young corpora lutea, but their primary product is progesterone.

The role of the corpus luteum has been known in a general way since 1903, when Fraenkel found that the removal of the corpora from the ovaries of the rabbit during the first few days of pregnancy usually causes the death and resorption of the developing embryos. Loeb (1907) demonstrated that the corpus luteum causes changes essential for implantation in the guinea-pig uterus, and in 1928 Corner and Allen prepared a

crude extract of the active principle. Progesterone was first isolated in pure form by Butenandt in 1934 and by a number of other workers during the same year and has the empirical formula $C_{21}H_{30}O_2$.

The corpus luteum hormone, progesterone, continues the uterine development and activity initiated by the estrogens; if this continued development does not take place, the developing embryo is unable to become implanted in the uterine mucosa and perishes for want of nutrients. There are numerous species and time differences as to the dependence of the embryo upon the corpus luteum. In the rabbit, removal of the corpora up to the eighteenth day results in the termination of pregnancy but in the guinea pig has no ill effects after the third day (Loeb, 1923). The ovary of the mare contains no functional corpora lutea during the latter third of pregnancy, whereas in the cow and goat removal of the corpus usually results in abortion. Evidence is now accumulating that the placenta may serve as an extraovarian source of progesterone during pregnancy, and it may be said that, with the possibility of a few exceptional cases, progesterone is necessary for the implantation and development of the fetus during pregnancy.

Progesterone causes uterine quiescence, and, while the uterus is under its influence, it is protected from the contractions that are normally stimulated by pitocin at the time of parturition. As will be discussed later, the corpus luteum is intimately concerned with the development of the lobule-alveolar system of the mammary glands, and it assists in the regulation of the estrual cycle. Progesterone inhibits the production of Graafian follicles, and, as long as functional corpora lutea are present in the ovaries, the anterior pituitary gland is prevented from secreting the follicle-stimulating hormone necessary for follicular development. Young and coworkers (1936) found that in the guinea pig estrogen and progesterone in proper proportions were more effective in inducing estrus than were estrogens alone, and Boling and Blandau (1939) have reported similar findings in the rat. These studies seem to indicate that, in some species at least, estrus, or sexual receptivity, is not dependent solely upon the female sex hormones but upon the production of small quantities of progesterone prior to ovulation by the cells lining the follicular wall.

As early as 1812, it was reported that the pelvic bones of the guinea pig undergo marked separation during pregnancy, and in 1926 Hisaw concluded that these changes were under hormonal control. The substance responsible for this phenomenon, relaxin, is present in rabbit blood as early as the eighth day of pregnancy and has been extracted from the corpora lutea of the sow in highly active form by Hisaw *et al.* (1930) and Fevold and coworkers during the same year. Marked species' differences in the anatomy and physiology of the pelvic region exist,

and whether relaxin is essential or even present in all mammals and what its relations with other hormones are, are only partially understood. Since relaxin is a component of the parturition complex, it will be discussed in more detail in subsequent paragraphs.

PREGNANCY AND PARTURITION

The anatomical changes and physiological processes that characterize pregnancy require a perfection in coordination which can be duplicated only by other biological phenomena. Nearly every body tissue is affected during gestation, and most embryologists agree that the miracle is the birth of a single normal young rather than the rare appearance of a monster. This perfect coordination is, for the most part, dependent upon the endocrine glands and their secretions, the hormones.

Uterine Functions.—As previously outlined, the development and maintenance of the nongravid uterus is regulated by the estrogens and progesterone, and the preparation for and the continuance of pregnancy are at least partially dependent upon these same hormones. It has been repeatedly demonstrated that the urine of pregnant women, cows, sows, mares, goats, and cats contains large quantities of estrogens, and this is the basis of certain laboratory tests for pregnancy. It has further been shown that the placenta contains appreciable quantities of the estrogens, and there is reason to believe that it may actually secrete the female sex hormones during pregnancy. The functions of the estrogens, which are secreted during pregnancy, are not clear-cut, but it has been suggested that they are concerned with uterine growth, that they assist in bringing on uterine contractions at parturition, that they assist in the regulation of progesterone secretion, and that they promote increased mammary growth.

The placenta of the human has also been shown to contain progesterone, and this finding, in combination with the knowledge that the ovaries of some animals may be removed during pregnancy without harmful results, has led to the belief that the placenta may be a source of progesterone. If progesterone is secreted by the placenta, its purpose is undoubtedly to supplement that produced by the corpus luteum, and its functions, as previously elaborated, are the maintenance of pregnancy and the completion of mammary development.

In addition to containing estrogens, the urine of the human, chimpanzee, macaque monkey, and cow and the blood of the mare have been shown to contain measurable amounts of gonadotropic hormones during pregnancy. The presence of these hormones in the urine of women as early as the third week of gestation is the basis of the Friedman and Ascheim-Zondek pregnancy tests, and the fact that the blood serum of the mare contains large quantities of these substances by the fortieth

day after conception makes it possible to detect pregnancy in equines. The placenta contains large quantities of the gonadotropic hormones, and there is little doubt that it is capable of secreting anterior pituitary-like gonadotropic hormones.

The functions of these gonadotropins of placental origin are at present unknown. It has been demonstrated that they have a marked effect on the ovaries of injected females, sometimes causing follicular growth, sometimes ovulation and luteinization, and sometimes luteinization in the absence of ovulation. Because they appear at the time of placentation, it has been suggested that they are concerned with the development and maintenance of the placenta; whatever their exact mechanism may be, it would seem logical to conclude that they are concerned with normal gestation in the species named.

Glandular Changes.—During pregnancy, the pituitary gland, particularly the anterior lobe, becomes markedly increased in weight and activity. As described in previous paragraphs, the hypophysis regulates the activity of nearly every, if not all, the endocrine glands in addition to assisting in the metabolism of carbohydrates, proteins, and fats, and one would expect it to be vitally affected by pregnancy. It maintains the corpus luteum of pregnancy in a functional condition, it regulates uterine activity at parturition, and it produces the hormones that act directly on the mammary glands to bring about their development and the actual secretion of milk.

In the human, and probably other species as well, the thyroid gland becomes markedly enlarged in 50 to 90 per cent of all pregnancies. Increased thyroid activity is necessary in order that the pregnant female may satisfactorily meet the needs of both her own and the tissues of the developing fetus. Insufficient thyroid activity may result in abortion or, in the case of farm animals, hairlessness, weakness, and high mortality during the first few days of life. Thyroid deficiencies are particularly common in the iodine-free areas of the United States, and livestock men in such regions supply pregnant females with iodized salt or potassium iodide to prevent the difficulties described.

The parathyroid glands, which are located on the surface of or adjacent to the thyroid, are directly concerned with calcium metabolism and indirectly with the regulation of phosphorus metabolism. The increased needs of calcium and phosphorus during pregnancy and lactation result in increased parathyroid activity. If calcium is not provided in sufficient amounts, because of dietary inadequacy or underactivity of the parathyroid glands, calcium will be withdrawn from the bones and increased nervousness or severe muscular tetany may result. Milk fever, which is in reality temporary calcium deficiency due to the sudden need of calcium for milk production, is most satisfactorily treated by the

intravenous injection of calcium gluconate, which supplies the body needs until the parathyroids become adjusted to regulating calcium metabolism at a new level.

The Mechanism of Parturition.—Although it is known that pituitary, ovarian, and placental hormones regulate pregnancy and parturition, uncomplicated parturition cannot be induced at will by the injection of single or combinations of hormones. The evidence at hand indicates that progesterone, either of corpus luteum or placental origin, inhibits the uterine-stimulating effects of pitocin and the estrogens during pregnancy and prevents the premature emptying of the uterus. During pregnancy, the estrogens are produced in ever-increasing amounts that reach a peak just prior to parturition. Their function is not fully understood, but it is believed that they play a part either in directly stimulating uterine contractions at term or in sensitizing the uterus to pitocin.

In addition to producing progesterone, the corpus luteum, at least in some species, secretes a second hormone, relaxin, which increases in concentration just prior to parturition and causes relaxation of the symphysis pubis. In the human, the pelvis sometimes becomes very unstable and individuals so affected find difficulty in walking. The general relaxation of the pelvic region noted in farm animals just prior to term is probably due to this hormone.

The greater part of the uterine contractions during labor are probably dependent upon pitocin, a posterior pituitary hormone. At the time of parturition, the uterus, no longer under the influence of progesterone and sensitized by the secretion of estrogens, is stimulated by pitocin to frequent and vigorous contractions that persist until the fetus and placenta have been expelled from the uterus. This pituitary hormone is frequently employed by obstetricians during the later stages of labor to hasten delivery and to control post partum hemorrhage.

THE DEVELOPMENT AND FUNCTION OF THE MAMMARY GLANDS

Turner (1940) states the importance of the mammary glands clearly and concisely:

> The mammary glands, unique structures common to all mammals, are an integral part of the female reproductive system. Just as the maternal placenta is the medium for the nourishment of the developing organisms during intra-uterine life, so the mammary glands continue to furnish maternal nourishment for the young for a varying period during extra-uterine life. The guinea pig is apparently the only mammal which is sufficiently mature at birth to make satisfactory extra-uterine growth without milk. The preparation for the change from intra-uterine nutrition by way of the mammary gland requires the highest degree of coordination and synchronization between the pituitary, ovaries, uterus, and mammary glands.

Gross Development of the Mammary Glands.—The anlage of the mammary glands appears early during embryonic development as a parallel thickening of ectoderm on either side of the central mid-line. Growth of this basic type of mammary tissue continues during gestation, and at the time of birth the young exhibits a very small mammary system composed chiefly of the number of teats characteristic of the species and a few primary sprouts that will later give rise to the duct system of the gland. During the period from birth to puberty, in farm animals, the mammary glands are relatively quiescent, and that increase in size which is observed is due chiefly to the production of connective tissue and fat.

The mature mammary gland is, in addition to such basic elements as blood, muscle, nerve, connective tissue, and fat cells, composed of two types of tissue: the ducts, which are concerned chiefly with the storage and transport of milk to the teat; and the lobule-alveolar system, which is concerned with the actual secretion of milk. The eventual size and function of the udder will depend, to a large extent, upon the amount and ratio of these two types of tissue.

Marked growth of the mammary system is not initiated until the time of puberty, and the amount of growth that takes place between puberty and pregnancy depends largely upon the species and its characteristic estrual cycle. Gardner and Strong (1935) have shown that the mouse, which has a short estrual cycle of 4 to 6 days, exhibits marked duct growth up to about 70 days of age and little further duct growth from 70 to 100 days. In the cow, which has an estrual cycle of 18 to 21 days, development of the ducts begins at puberty and continues more or less rhythmically prior to pregnancy. Although the mammary development of sheep and goats, which are seasonal breeders, has not been completely worked out, studies of Deanesly (1934) on the hedgehog have shown that at the beginning of the breeding season the mammary glands of females which had lactated the previous year were made up of only a thin network of ducts, and that the ducts and lobules necessary for full lactation would have to develop after the onset of the breeding season and during pregnancy.

Mammary development proceeds at a rapid rate following conception. Hammond and Marshall (1914) and others have shown that, in the primiparous rabbit, duct growth continued and that by the mid-period of pregnancy the lobule-alveolar system had developed and secretory activity had been initiated. Turner, Gomez, and De Moss (1933–1936) have studied mammary development in the mouse, cat, dog, and goat, and report that when virgins with well-developed duct systems are bred, the first half of pregnancy is devoted to the rapid development of the lobule-alveolar system and the second half of pregnancy is characterized by an enlargement of the epithelial cells of the lobules and the secretion

of a fluid into the alveolar lumina. Considerable increase in udder size and turgidity is observed during the second half of pregnancy but this is not true growth, as was formerly believed. The actual increase in mammary tissue, hyperplasia, occurs, as previously stated, during the first half of gestation, and the increase in size during the last half is due to the accumulation of the secretory products of the lobule-alveolar system and should be classified as a type of hypertrophy.

The Endocrine Control of Mammary Development.—Although it has been known for nearly two decades that the pituitary gland, the ovaries, and uterus are concerned with the development of the mammary gland, the exact relations of these organs have been and still are only partially

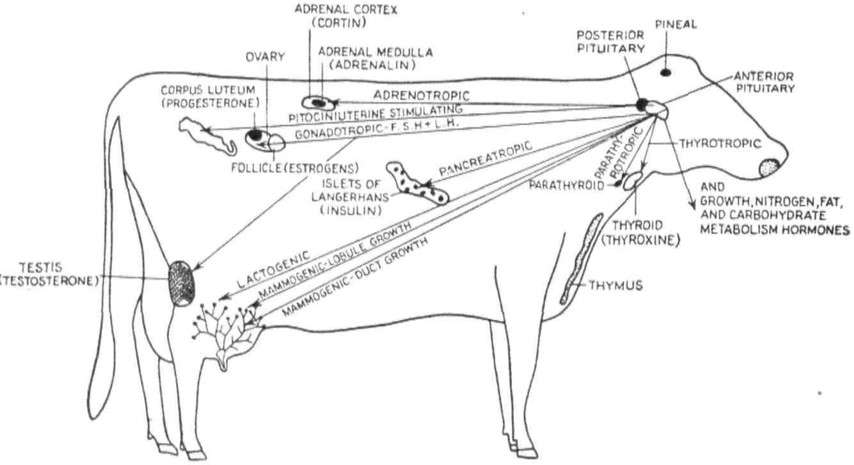

FIG. 48.—Diagram showing the relative location of the principal endocrine glands and their principal hormones.

understood. Allen *et al.* (1924), Turner and coworkers (1932–1934), and others have shown that in normal mice the injection of estrogens is followed by rapid duct growth. Similar findings have been reported by others for rats, rabbits, and dogs. In the normal guinea pig, estrogen induces not only duct growth but development of the alveoli as well (Turner and Gomez, 1934), and it was later demonstrated that the monkey responds similarly. When estrogens were injected into hypophysectomized guinea pigs (Lyons and Pencharz, 1936) (Gomez and Turner, 1936–1937), nipple growth was stimulated, but the glands were not affected.

Similar results with rats (Reece, Turner, and Hill, 1936) and the substantiation of their findings by others led to the hypothesis that the estrogens do not affect the mammary glands directly but influence the pituitary to secrete hormones which are specific in causing mammary

development. This hypothesis was strengthened by the observations of Gomez, Turner, and Reece (1937) that in the hypophysectomized guinea pig the daily implantation of a male-rat pituitary plus estrogen caused mammary growth but, in the absence of estrogen, no stimulation. Lewis and Turner (1939) have made a thorough study of this problem and have substantiated the belief that the pituitary secretes a mammogenic-duct growth-stimulating hormone and that the production of this hormone is probably due chiefly to the action of estrogens on the hypophysis. These workers found that the pituitaries of cattle of all types, sexes, and physiological conditions contain some mammogenic-duct growth hormone, that the pituitaries of heifers over 500 lb. with corpora lutea in the ovaries have a higher content of the duct growth factor than any other group of cattle studied—thus lactating cows were a richer source than nonlactating, nonpregnant cows—and that dairy cows produce more of this hormone than beef cows.

Ancel and Bouin (1911) suggested that the corpus luteum is responsible for mammary growth during the first half of pregnancy in the rabbit, but Corner (1930) and Turner and Frank (1931) were unable to stimulate either duct or alveolar growth in the rabbit by progesterone alone. During the same year, Turner and Frank injected progesterone and estrogen simultaneously into castrated male rabbits and produced growth characteristic of that observed during the first half of pregnancy. Turner and coworkers later demonstrated the same effects in rats, mice, and cats. It was subsequently found that male or female rats or guinea pigs do not respond to estrogens and progesterone after the removal of the pituitary. Gomez and Turner (1937) and these workers theorized that the hypophysis secreted, in addition to a duct growth factor, a mammogenic lobule-alveolar hormone. Recent work by Turner, Mixner, and Lewis (1939–1941) has provided additional evidence that the anterior pituitary, under the influence of estrogens and progesterone in combination, does secrete a mammogenic factor which brings about the final development of the alveolar system.

Briefly, in review, at the time of puberty and during early pregnancy, estrogens stimulate the anterior pituitary gland, which, in turn, secretes a mammogenic-duct growth hormone. During the first half of pregnancy, estrogens and progesterone acting in combination cause the pituitary to produce a second substance, the mammogenic lobule-alveolar growth hormone. As a result of stimulation by the mammogenic hormones, the mammary gland is anatomically developed by the mid-point of gestation.

The Endocrine Control of Lactation.—Grueter (1928) was the first to demonstrate that the anterior pituitary gland is essential for normal lactation, and Grueter and Stricker (1929) showed that sows which produce little or no milk after parturition could be induced to lactate by the

injection of an anterior pituitary extract. The substance in the hypophysis responsible for the initiation of secretion by the properly developed mammary gland was first isolated by Riddle, Bates, and Dykshorn (1932–1933) and is now generally known as the *lactogenic hormone* In order to be capable of response to the lactogenic hormone, the mammary system must have been previously developed by the action of the mammogenic hormones. Lactation is prevented in the absence of the lobule-alveolar system. Asdell (1931) was, for this reason, unable to induce milk production in the male or immature female rabbit, and Turner (1931) reported that heifers could not be stimulated prior to puberty, whereas, after a number of estrual periods had taken place, the injection of lactogenic hormone was followed by limited secretion. Turner and De Moss (1934) demonstrated that if the mammary glands of male cats are first stimulated by estrogens and progesterone, abundant lactation is induced by the injection of lactogen.

That the lactogenic hormone is responsible for the initiation and continuance of milk secretion is a generally accepted fact, but the mechanism that suppresses the secretion of this hormone during gestation and stimulates its production after parturition is not perfectly understood. Some workers believe that during pregnancy a definite substance, probably a hormone, is present in the blood stream and prevents the production of the lactogenic hormone, or that it is a reciprocal relation among the ovarian, pituitary, and placental hormones.

Reece and Turner (1937) found that the anterior pituitary glands of females contained more of the lactogenic hormone than those of males and that dairy cattle were a richer source than beef cattle. In rats and guinea pigs, following parturition, the lactogen content of the pituitary was more than doubled; castration of the female rat resulted in decreased lactogen secretion; and the injection of estrogens increased the secretion of lactogen. When young were permitted to suckle female rats, either with or without the removal of milk, the amount of lactogen in the pituitary was decreased, tending to show that the lactogenic hormone is released into the blood stream for purposes of stimulating milk production by the act of suckling.

Substances other than lactogen are vitally concerned in milk secretion. Grimmer (1918) showed that thyroidectomy resulted in decreased milk production in the goat, and Graham (1934) demonstrated that the administration of desiccated thyroid tissue or thyroxin to cows during the declining phase of lactation was followed by increased milk flow. Ralston, Cowsert, Turner, *et al.* (1940) found that the injection of thyroxin resulted in an average increase in milk yield of 13 to 18 per cent, an average increase in total pounds of fat of 22 to 24 per cent, and an increase in percentage of fat of 4.30 to 4.75. Reece and Turner (1937)

reported that the anterior pituitary glands of dairy cattle contained appreciably more thyrotropic hormone than did those of beef cattle, and this, in combination with the fact that dairy-cattle pituitaries contain more lactogenic hormone than those of beef cattle, tends to explain the differences in milk production.

The cortical hormone, which is secreted by the cortex of the adrenal gland, is also apparently essential for lactation. Carr (1931) showed that lactation was terminated within 2 or 3 days after adrenalectomy in the rat. Gaunt and Tolin (1936) found that amounts of the cortical hormone sufficient to maintain life in the rat did not sustain lactation, but that, when the dosage was doubled, lactation was maintained. The

Summary of the Endocrine Glands and Their Chief Functions

I. Pituitary gland.
- *A*. Anterior-lobe hormones.
  1. Growth.
  2. Gonadotropic—follicle-stimulating and luteinizing hormones.
  3. Thyrotropic.
  4. Adrenotropic.
  5. Lactogenic.
  6. Mammogenic—duct and lobule-alveolar factors.
  7. Parathyrotropic.
  8. Pancreatropic.
  9. Nitrogen metabolism.
  10. Carbohydrate metabolism.
  11. Fat metabolism.
- *B*. Posterior-lobe hormones.
  1. Pitocin—uterine-stimulating.
  2. Pitressin—blood-pressure-regulating.
  3. Metabolic.
- *C*. Intermediate lobe.
  1. Pigmentation hormones.

II. Testis.
- Testosterone regulates:
  1. Growth and maintenance of genitalia.
  2. Secondary sexual characters.
  3. General body growth.
  4. Regulation of other endocrines.

III. Ovary.
- *A*. Estrogens regulate:
  1. Growth and maintenance of genitalia.
  2. Secondary sexual characters.
  3. General body growth.
  4. Indirect regulation of estrual cycle.
  5. Assistance in development of mammary glands.
  6. Regulation of other endocrines.
- *B*. Progesterone regulates:
  1. Preparation of genitalia for pregnancy.
  2. Assistance in development of mammary glands.
  3. Regulation of other endocrines.

C. Relaxin regulates:
1. Relaxation of symphysis pubis in late pregnancy.

IV. Thyroid.
Thyroxine regulates:
1. Metabolic processes.
2. Body growth and differentiation.
3. Reproduction to some extent.
4. Lactation to some extent.

V. Parathyroids regulate: calcium metabolism.

VI. Adrenals.
A. Medulla. Adrenaline regulates:
1. Blood pressure and heart rate.
2. Certain types of muscular contraction.
3. Metabolic processes.

B. Cortex. Cortical hormones regulate:
1. Sodium, potassium, and nitrogen excretion.
2. Water metabolism.
3. Relations with other endocrines.

VII. Pineal—possibly regulates growth and sexual development.

VIII. Thymus—possibly regulates growth and sexual development.

IX. Pancreas—islands of Langerhans.
Insulin regulates:
1. Blood-sugar level.
2. Formation and storage of liver glycogen and muscle glycogen.

X. Placenta.
Has been shown to contain:
1. Estrogens.
2. Progesterone.
3. Gonadotropic hormones.

adrenal cortical hormone is concerned, among other functions, with the maintenance of normal sodium chloride and water levels in the blood stream, and it is believed than an insufficiency of this hormone reduces the precursors of milk available to the mammary gland and thus limits or prevents lactation.

Summary.—In this chapter we have tried to account for the mechanisms that regulate the development and functions of the reproductive organs and the mammary glands. We have learned that the pituitary, a tiny endocrine gland located near the geometric center of the skull, produces at least 18 distinct substances, either directly or indirectly controls general body growth, reproduction, lactation, and the functions of numerous other endocrines, and is concerned with nearly all types of body metabolism. We have seen that reproduction and lactation are not specific or independent functions but are dependent upon the coordinated activity of nearly every body tissue, particularly the endocrine glands and their hormones. When we consider that the science of endocrinology has, for the most part, been developed since 1920, we marvel at the fact that we have learned so much about these intricate

functions rather than that we cannot yet explain certain phenomena. We should not be impatient with the failure of certain types of endocrine therapy to solve all our reproductive problems but grateful for the immense help that the endocrines have given man and beast.

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CHAPTER VII

FERTILITY

For the breeder there is no more important economic problem than the fertility of his animals. Animals are simply natural machines that man has domesticated and improved for the purpose of turning feed into power, meat and/or milk, meat and wool, meat and/or eggs, or just meat alone, all these qualities except power and wool being dependent on fertility. Some other animals, of course, are bred for sport, companionship, or for the purpose of giving vent to an expression of one angle of man's aesthetic nature. In short, animals are bred for utility or fancy or sometimes both, though in this book we are concerned primarily with those bred for utilitarian purposes.

Every animal in a breeding herd or flock that either temporarily or permanently loses its fertility is a financial burden upon its owner. To live, they must be fed and cared for, and any period of infertility means financial loss. Breeding animals of the meat classes that do not bear young annually are plainly liabilities for these years. Dairy cattle that fail to conceive within 3 to 4 months following their last calving are also apt to be liabilities for at least part of the year. There is undoubtedly a small yearly loss in every herd and flock in the United States due to breeding efficiency not reaching 100 per cent, whereas the total loss from this cause must be very large. The question of fertility is second to none in breeding, for an animal's individual merit and genetic prepotency to stamp its good qualities on its offspring are greatly reduced in value or completely lost if the said good animal leaves few or no offspring.

Definitions.—Fertility is the ability of the male to inject copious numbers of viable spermatozoa into the female genital tract at each service and the ability of the female to produce one or many viable eggs and to provide a suitable environment for the processes of fertilization, implantation, and fetal development, and finally to succeed in safely delivering the completed embryo to the outside and providing suitable care and nourishment until the young can fend for themselves.

Fecundity, meaning fertility or prolificacy in a general sense, comes from the same root as fetus, and for this reason its use is more or less restricted to females.

Prolificacy implies especially frequent or especially large numbers of offspring and is also more or less restricted in its application to the female.

In all the higher species the production of young is contingent upon the union of viable germ cells from both parents. In those species, however, which normally produce more than one offspring at a time, pro-

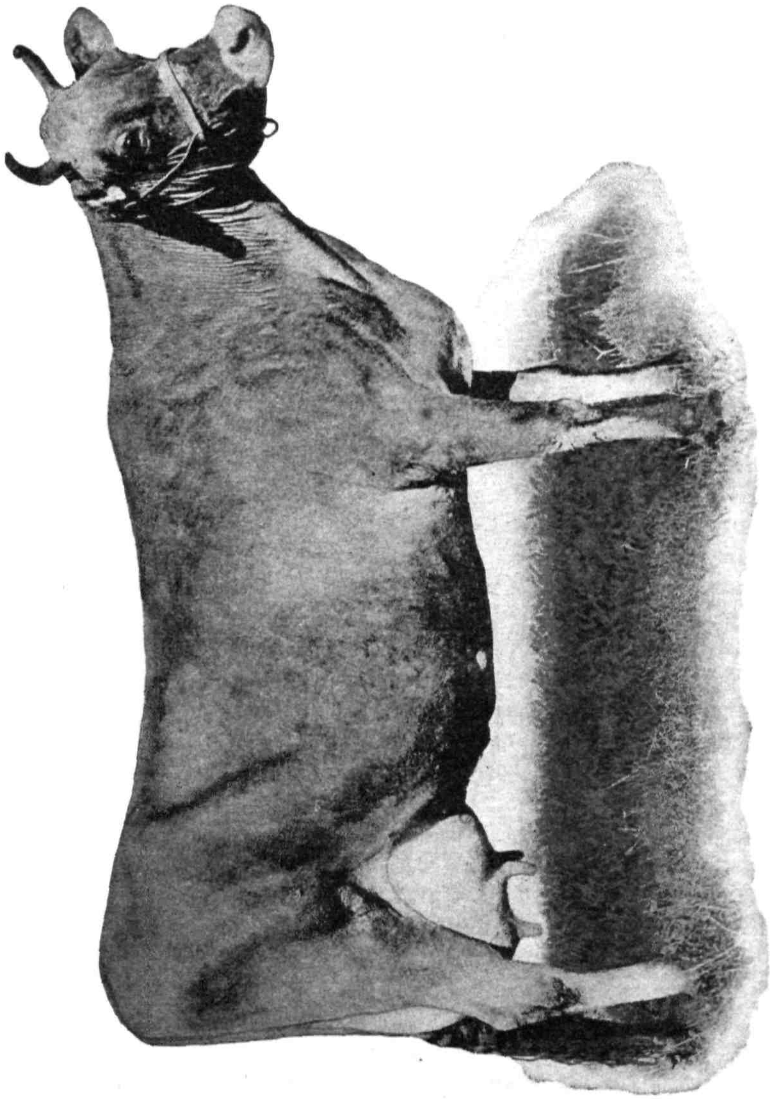

Fig. 49.—Financial King's Interest, a Jersey cow that produced 20 heifers and 1 bull calf. (*Courtesy American Jersey Cattle Club.*)

lificacy is measured through the fecundity of the female, for the reason that a fertile male produces enough spermatozoa at a service to fertilize billions of ova. In swine the number of pigs per litter depends not on

the boar, provided he is producing viable spermatozoa, but upon the number of ova that have matured in the sow's ovaries. Likewise a ram, granted normal breeding health, cannot affect the number of twin or triplet births, for this depends on the number of ova produced by the ovaries of the ewe. Nevertheless, the inherited power to produce large litters in hogs or twins in sheep can be transmitted by the boar or ram to his offspring, and its effects make their appearance in the second generation. For this reason, it is wise to select boars from large litters and rams from twins, other things being equal or being given due consideration. In any case, males should only be selected from naturally fertile strains, which can be determined, of course, only by complete records of the ancestors and collateral relatives.

There are two influences at work in the manifestation of fertility, one intrinsic, or genetic, the other comprising all the influences both internal and external to the animal that are extrinsic to the genes themselves, *e.g.*, the states of nutrition, health, system of management, etc.

Before proceeding to a discussion of the various factors that promote fertility, it seems wise to consider in broad outline the reproductive phenomena in each of the various classes of farm animals. The initial production of reproductive cells, spermatozoa or ova, brings about the well-known change in the individual known as *puberty*.

Puberty.—Animals reach physiological maturity, bone and muscular growth complete, at varying times in the different classes of animals and in different breeds within the classes. Sexual maturity, in the sense of the ability to produce viable germ cells though not necessarily or usually at the maximum rate, is reached much earlier. The sexual function seems generally to make its appearance when the animal is about one-third of the way along in weight between birth and full growth. In the young, growing animal the primary organs of reproduction, testes and ovaries, are present and functioning at a low level. The initial stages of spermatogenesis and ovogenesis are in operation, but the process at this time does not carry through to completion, and the amount of gonad hormones produced is below the level required for rapid growth of the accessories and the appearance of secondary sexual characters.

As body growth begins to slacken the anterior-lobe hormone transfers its influence to the sexual apparatus. This onset of sexual activity is known as *puberty*. The growing testes and ovaries now produce more of their particular hormones, the accessory organs spurt in development, the secondary sexual characters begin to make their appearance, and viable eggs and sperms begin to be produced. Full reproductive capacity, of course, comes later.

In the horse, puberty occurs at about one year; in cattle at four to eight months; in the sheep at four to eight months; and in swine at

three to six months. The exact age at which puberty is attained varies considerably in different breeds, the smaller ones generally having an earlier onset than the larger, slower maturing ones. The onset of puberty is very greatly influenced by nutritional and environmental factors, and, as stated above, it occurs in general when animals have reached about one-third of their adult size.

However, animals should never be bred at puberty, and the sexes should early be separated in order to remove the possibility of pregnancy in the females. Dukes reports the case of a heifer giving birth to a calf at 364 days of age and it is not unusual for heifers to calve at fourteen to eighteen months of age and for sows to pig at six to nine months. It has been demonstrated that gestation itself does not retard growth, in fact, may stimulate it. But the following lactation may seriously retard growth, and too early pregnancies should therefore be avoided.

Likewise it is not advisable to delay breeding too long beyond puberty, for in practice this is found often to result in partial or complete sterility, in spite of authenticated exceptions such as mares conceiving to their first service at sixteen years of age. In general the males of most farm-animal classes can be used for light breeding service before it would be wise to breed the females.

Indications of Puberty.—Hypophyseal stimulation of the ovaries and testes conditions the onset of puberty. This is accompanied by marked psychological changes also. In both sexes there ensues a desire to mate, and the male now really begins to "feel his oats." Good management assumes that males are handled more or less from birth onward. If they are not handled before puberty, the task of making them tractable and safe to handle is a particularly difficult one. For maximum breeding efficiency, males, except under range conditions, should be trained to lead or to obey, for their ultimate breeding worth and the safety of caretakers can thereby be greatly enhanced.

Signs of puberty or of estrus are evident enough in some species and rather obscure in others. In the mare, one notices frequent urination, also neighing and friendliness toward the stallion if he is brought near. In cattle, the heifers are nervous, riding other cattle if opportunity presents, and do considerable bellowing but exhibit little swelling or bleeding at the vulva. Sows at this period eat sparingly, are extremely restless, and have noticeable swelling and congestion of the vulva. Ewes that are in heat show some vulval swelling and mucous discharge but will be discovered most readily by "turning in" the ram each morning during the breeding season. In all constructive breeding, it is essential to know the sire and date of service, which means that one must, except under range conditions, practice "hand coupling" rather than letting the male run at large with the females.

Normal Breeding Season. Age at First Breeding. Gestation.—All classes of farm animals are normally timed by nature, probably evolutionarily through differential survival rates, to drop their young, in temperate regions, in the spring, because climatic conditions are favorable at this season, and also because there is then abundant food for both mother and offspring. This feature brings the normal breeding season as many months previous to spring as the gestation period covers.

Mares are polyestrus for part of the year, generally from March through July and sometimes on into the fall months. Fillies generally start coming in heat when they are one year old, although they are seldom bred until at least two years of age and more often not until they reach their third year. The estrus period is more variable in this species than in any other class of farm animals, ranging from 2 to 11 days, according to Dukes, with an average duration of 6 days. Ovulation is now known to occur from 24 to 48 hours before the end of the heat period, and in this the ovaries do not necessarily alternate.

On the range, mares are usually served many times during one estrus and, due at least in part to this, the conception rate is often as high as 90 per cent, whereas under "hand coupling" it is only about 50 per cent. This latter low figure is undoubtedly largely due to mating at times too far-removed from ovulation. Sperm live only 1 to 3 days, and the egg is capable of fertilization for probably only a few hours after ovulation. Service too early or too late in estrus will therefore be unavailing. It is recommended that mares be bred on the second, fourth, and sixth days of heat or on the third and sixth days. After foaling, mares generally come in heat in from 4 to 11 days. This is known as the *foal heat.* During the estrual season, mares come in heat about every 21 or 22 days.

This time, however, is variable, and, if a mare has long heat periods of, say, 10 days, she will come in heat about every 26 days. Hammond has made the observation that in most cases there will be a period of 16 days between going out of heat and coming in again. They are generally bred first at three years of age and with good care should be regular breeders for 10 or 12 years at least. The gestation period in mares ranges from 300 to 400 days with an average of about 336 days, or 48 weeks, in the heavy breeds, somewhat longer in Thoroughbred or other light breeds (Lambert *et al.* report 343.7 ± 8.9 days for Morgans), and longer also when a mare is carrying a mule foal, the regular period in the ass family being about 365 days. Foals born early in the spring are apt to be carried up to 15 days longer than 336 days; those in the summer up to 15 days shorter than 336 days (Hammond). Stud foals are generally carried a little longer than fillies, and the gestation period of twins is likely to be shorter than usual.

In mares about 1-month pregnant there is generally a large corpus luteum and many large follicles in the ovaries. At about 3 months the follicles change to corpora lutea without rupturing, whereas at about 6 months the corpora lutea have generally all disappeared. Follicles start to develop again just previous to parturition, which provides the egg for foal heat.

Cows will breed at all seasons of the year; in other words, cattle are polyestrus. Heifers start coming in heat at from four to eight months of age depending largely on their rate of growth. Heifers are generally bred at from twelve or fourteen to twenty-two or twenty-four months of age. The estrus period in this class of animals is variable (6 to 30 hours), ranging from 16 hours in heifers to 20 or 24 in older cows, and its manifestation and length are variable with the season, being shorter and harder to detect in winter and especially when cattle are kept stanchioned. Ovulation takes place at the end of or the day following heat, and usually only one follicle fully matures, although several approach maturity, and sometimes two, three, or very occasionally four fully mature. As in the mare, the ovaries do not necessarily alternate in ovulation, but the right ovary functions slightly more often than the left.

Mature, viable follicles are tense when palpated per rectum, soft ones being either atretic or pathological. Unlike the mare, there is but little hemorrhage in the follicle following ovulation. After calving, cows may come in heat in from 16 to 90 days, but most usually this occurs at from 40 to 50 days and more or less regularly thereafter at 19- to 20-day intervals. Heifers are generally bred to calve first at about two years of age and should remain regular breeders for 8 to 10 years at least. The gestation period in cows ranges from about 270 to 290 days, with the average at 281 days. Bull calves are generally carried a little longer than heifers.

If the corpus luteum is squeezed out of a cow's ovary at 8 to 12 days following heat, another follicle will mature in from 2 to 6 days. In this manner a group of animals could be brought into heat at approximately the same time. Injection of gonadotropic hormone will cause heat in about 24 hours, but this is ineffective if a corpus luteum is present (Hammond).

Ewes, like the mare, are seasonally polyestrus, although, in Merinos and Dorsets, heat periods often occur at any time of the year, this being utilized in the latter breed for the production of "hot-house" lambs, which are born in the late summer or early fall. The usual breeding season for ewes extends from September to December in the Northern Hemisphere. Ewe lambs often come in heat but generally are not bred until they are yearlings or shearlings at about eighteen months of age. The length of estrus in sheep ranges from 1 to 3 days, increasing gradually

with age, with an average of from 30 to 36 hours. The average interval between heats is 16 to 17 days. Ewes are generally bred each fall and have generally outlived their usefulness as breeding animals by the time they are five to seven years old. The gestation period in ewes varies from 140 to 160 days, with an average of 147 days for middle and long-wooled breeds and 152 days for the fine-wooled. The larger breeds bear more twins and triplets than the smaller ones, and this proclivity to multiple births is especially susceptible to nutritional manipulation.

As the breeding season approaches, ovulation may occur without visible signs of heat. The injection of prolan (pregnant women's urine hormone) or pregnant-mare-serum hormone during the nonbreeding season also causes ovulation without heat. It has been found (Cole and Miller, Hammond) that a second injection in 16 days will cause ovulation, heat, and the possibility of conception if bred or that the first injection followed by artificial insemination may result in conception (Zawadowsky *et al.*)

Goats are closely related to sheep, show a little longer estrus period with intervals between heats averaging 19 to 21 days, and the gestation period is 1 or 2 days longer.

Sows will breed at practically any season of the year, but in general practice they are usually bred in November or December and in May or June. Puberty is reached in this class of animals at from three to five months, making the early separation of sexes highly important. Gilts are usually bred first at from nine to ten months of age but in no case should they be bred until they have reached a weight of from 180 to 200 lb. The estrus period ranges from 1 to 5 days, with the average at 2 to 3 days. Ovulation has been shown to take place during the latter stages of estrus, about 30 to 36 hours following the initial onset of heat, so that mating is generally practiced on the second day of heat. A large but varying number of follicles mature in each ovary at heat, the combined output ranging from 15 to 40. Some of them, perhaps, are never fertilized, some fail to become implanted, and some are absorbed at varying stages of pregnancy. There are practically always more corpora lutea in the ovaries of a pregnant sow than pigs in the horns of the uterus.

After pigging, sows generally come in heat in 3 to 5 days but for obvious reasons should not be bred at this time. Sows will come in heat 3 to 5 days following weaning no matter at what age the pigs are weaned, though for best results they should not be weaned until they are eight weeks old. The period between heats ranges from 18 to 24 days, with 21 as the average. Good sows should be kept in the herd as long as they continue to produce and wean big litters of vigorous pigs, which generally means till they are five to seven years old. The gestation

period in sows ranges from 110 to 116 days, with the average at 113 or 114 days.

Fertility and Age.—We might chart the fertility, *i.e.*, the ease with which females conceive and the number of young they produce in a given period of time, of any species of animals. If we did so, our chart would progress along the zero line until age of puberty. It would then rise sharply and continue to rise for some months or years, gradually flattening out into a straight line. Eventually, of course, it would begin to decline and finally reach the zero line again. The breeding history of a sow will illustrate this point. At birth, the sow pig is sterile. She may come in heat and be successfully bred, say, at eight months and perhaps produce a litter of 7 or 8 young. Her next few litters will normally increase in numbers until she reaches her maximum of 12 to 14 young at about three to four years of age. After that, the litters are quite likely to become smaller, and she may become completely sterile at about eight or nine years of age.

McKenzie and Terrill found that the ovulation rate in the ewe with respect to age fell into three phases: (1) lambs and yearlings had a mean ovulation rate of 1.21; (2) ewes three and four years old, a mean ovulation rate of 1.61; and (3) those in the five- and six-year-old age groups had an ovulation rate of 1.46.

Keith reports that size of litter in hogs increases with age of dam up to four and a half years, followed by a gradual decrease. Fertility was not affected by the age at which they were first bred, but for obvious reasons all breeding animals should begin to function in reproduction as early as is consistent with sound principles of health and management.

Bowling, Putnam, and Ross have analyzed the breeding records of the dairy cattle at the West Virginia Agricultural Experiment Station for the influence of the age of the bull on number of services required per conception. There was practically a steady rise from 1.5 services per conception by bulls one to two years of age, through 2.0 services per conception by bulls seven to eight years of age, up to 2.5 or more services required by bulls twelve years and over for each conception. The author's suggestion is that heifers be mated to young bulls for their first conception in order to avoid the loss of too much time in getting them with calf.

Morgan and Davis in a study of the cattle in the University of Nebraska herd found that fewer services per conception were required from young bulls under two years of age and that the services required from bulls two to eight years of age were a little higher and quite uniform. Data from bulls over eight years of age were not extensive enough to permit conclusions. Their study also revealed that virgin heifers required more services per conception than any other age group of cows from age two to thirteen years with the exception of those in the ten-

apart have been reported in the *Journal of Heredity*. Identical twins are rare or missing in horses, sheep, and swine and reported by Johansson to make up 6 per cent of twin births in cattle. Henning reports such a case in sheep.[1] Bonner and Skarman suggest the use of hair form as an aid in the identification of monozygotic twins in cattle.[2] Identical twins are always of the same sex.

Fraternal twins may be of the same or opposite sex. They arise from the union of separate ova and sperm and are therefore no more alike than ordinary brothers and sisters.

The now extinct famous strain of Bates Duchess Shorthorn cattle was highly prized for its excellence, and breeders practiced inbreeding in this family to intensify these favorable characteristics. They were successful in this, but from the start the strain was marked by barrenness, the full expression for which the inbreeding also provided, so that after a few generations the strain entirely disappeared. A certain strain or family of animals is more fertile than another because of its hereditary complex, owing, in all probability, to differential rates of production and reactivity of the hormones underlying sexual manifestations and to lethal genes that prevent the normal processes of fertilization, implantation, differentiation, and organization of the embryo. Inasmuch as we have no means for the direct examination of the hereditary complex, the best one can do is to study the way in which it manifests itself and make his selections accordingly. As will be mentioned later, this feature of fertility should receive due consideration in all selection procedures.

Fertility and Conformation.—When the broad problem of fertility in the animal kingdom is viewed, there is seen to be a general correlation between the size of the animal, its gestation period, and its fertility. In those species in which the gestation period is of longer duration than 6 months, the normal number of young at a birth is 1, whereas in those species in which the gestation period is less than 6 months several young are usually produced simultaneously. In general, the smaller the species the more young are produced. Although this relation holds between species, it does not hold within a given species; *i.e.*, the smaller animals within a species are not the most fertile. In fact, just the contrary is true. In swine, for instance, the sows of the Yorkshire breed produce larger litters than those of the smaller Essex breed. The conformation of the former, which is long, roomy, and deep, favors large litters. The same general proposition holds with sheep. This conformation in all females, *viz.*, roominess of middle, for both feeding and breeding purposes, cannot be overstressed. In the human family, the investigations of Galton in England have demonstrated that "daughters are not taller

[1] *Jour. Hered.*, February, 1937. A list of other references on this topic is included.
[2] *Jour. Hered.*, July, 1938.

than their mothers, but they are taller than wives in general," which is but another way of saying that the taller women are the more fertile. These conditions are what would be expected because space is required for the normal development and housing of the generative organs and, more especially, for the successful development of an embryo. Theoretically, because anterior pituitary hormones stimulate growth or lengthening of body as well as later reproductive functioning, it would seem that greater fertility and longer bodies may both be the end result of greater anterior-lobe pituitary activity. A breeder should use due caution in selecting breeding animals, seeing that they are of suitable conformation for their task, as well as that they are selected from a naturally fertile strain.

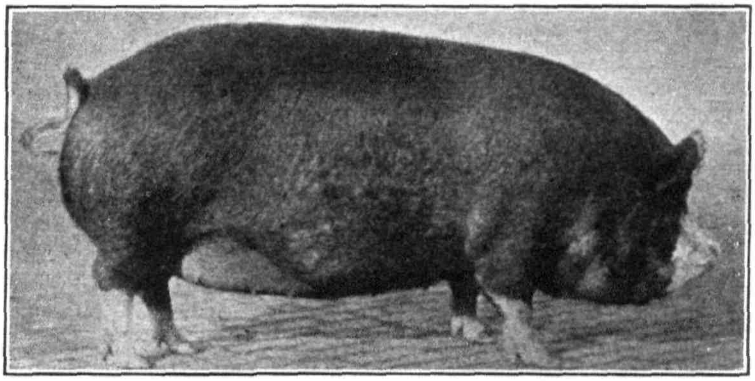

FIG. 52.—Double's Duchess 5th, a Hood Farm bred Berkshire sow. Her conformation won her a grand championship at the International and is of the kind generally conducive to fertility. Long-bodies hogs are best from the packers' standpoint also, as they yield a greater amount of the valuable cuts.

Fertility and Management.—Many features of this problem would seem to fit better into the chapter on reproductive efficiency. We will, therefore, limit our consideration at this point to but one feature of management, *viz.*, exercise.

Exercise of the bulls at the Government Experimental Farm was instituted many years ago in order to try to increase the breeding efficiency of old proved sires. Other measures to help achieve the same end were also used, so it is difficult to measure exactly the contribution to the breeding health of these animals that accrued from exercise. That their breeding health was enhanced through forced exercise, however, can hardly be denied. The driving of cows on a track for 2 hours daily over periods of from 30 to 156 days seemed to be the causative agent in bringing 11 out of 19 previously sterile cows into a renewed state of fertility.

For the maximum functioning of the generative tract of both males and females, good bodily vigor is essential. All breeding males should

be made to exercise if they will not do so voluntarily. The same is true of females. Lowered muscular tone throughout the body is undoubtedly reflected in the generative tract just as disease or lowered tone there would be reflected in the rest of the body. Stallions can and should be worked, bulls can be run together in good-sized lots, boars and rams can be so housed and managed that they are forced to get some exercise, and in these ways the breeding efficiency of the average sire can be increased.

With the female, exercise will not only make her more likely to conceive readily but, if continued through the gestation period, will result in a more vigorous offspring. An item of such simple and inexpensive nature is quite likely to be overlooked by the average breeder. If due

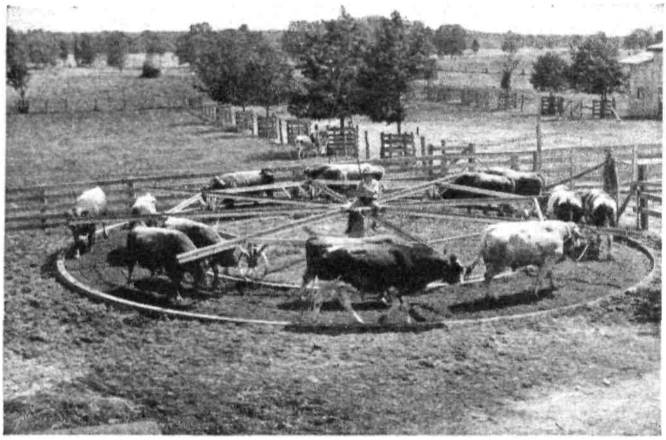

FIG. 53.—A method for exercising bulls in use at experimental farm, Beltsville, Md. (*Courtesy Bureau of Dairy Industries, U.S. Department of Agriculture.*)

attention were paid to this feature of management, the breeding efficiency in the average herd or flock could undoubtedly be raised many per cent and at little or no cost. The best condition for a breeding male is commonly said to be a *hard* one, meaning that the male should be fairly lean and hard. Without suitable exercise, this state is impossible of attainment.

In the case of horses and dairy cattle a dual function is expected of the animal. That is to say, we expect a return in work from the mare, and sometimes from the stallion as well, and a return in milk production from the cow, as well as returns from both species in the form of offspring. The breeder's aim should be to strike a balance between these two demands of production and reproduction. Oftentimes this balance is disturbed, especially with dairy cows. They are forced to such high milk production that the reproductive processes are seriously interfered with, sometimes only temporarily, at other times permanently.

Fertility and Nutrition.—That the state of nutrition of an animal has an influence upon its reproductive powers is too well-known to require great elaboration. A certain minimum of nourishment is essential for the well-being of any individual, and the reproductive function will not be manifested until after the minimal nutritional needs of the individual for survival have been met. After this threshold has been passed, there will be a steady rise in the reproductive powers of the individual until its natural limit has been reached.

It was formerly thought that continuing to raise the plane of nutrition so that animals laid on considerable fat would cause a lowering of fertility or perhaps sterility. This view is now being questioned, and there is no absolute proof either way at present. It may be that the sterility of a great many grand champions was due only indirectly to their high plane of feeding, leading to inactivity, varying degrees of autointoxication, or fatty infiltration of the organs or parts of the genitalia. These sequelae to overfeeding may have been the real cause of temporary or permanent sterility. Friedman and Turner of the Bureau of Dairy Industry ask whether fatness may not be due to sterility rather than the other way around.

It has been hard to test the effects of various components of physiologically incomplete rations on fertility, because, generally, when the ration is lacking in some constituent, its palatability is lowered, appetite fails, and the food intake is low. It is well-known of course that inanition or starvation rather quickly leads to degeneration of the seminiferous tubules and Graafian follicles and finally affects both the primary and secondary organs of reproduction in both sexes.

For normal growth, the ration must contain sufficient amounts of energy (carbohydrates, fats, and protein), proteins suitable as to quality as well as quantity, minerals, and vitamins. There is no evidence that starches and sugars from whatever source show any qualitative differences for either growth or reproduction. In the rat, it has been shown that fat-free diets do eventually stop estrus and ovulation but not until the animals become emaciated and show other bodily derangements. The addition of small amounts of fat to animals so treated results in a restoration of the reproductive functions long before there is any noticeable improvement in general health.

Reproduction in the rat has also been shown to be very sensitive to low quality or incomplete proteins, the rabbit less so, and the larger domestic animals still less. Proteins are, of course, made up of some 20 amino acids, and, unless the essential acids are present, maximum growth cannot be attained. Whether this also holds for maximum reproductive activities in farm animals is not definitely known, but the feeding of a variety of high-qualified proteins could certainly do no harm.

Rations higher in proteins than usually fed have been shown to produce much faster gains and greater fecundity in both rats and rabbits, but with the larger farm animals a lower protein intake than optimum from the animal's standpoint may result in greater financial profit to the farmer.

Flushing, or the feeding of additional amounts of a high-quality and high-protein ration, or the turning of animals into particularly good pasture has been practiced by shepherds for a long period of time. It results in a larger lamb crop because the good feeding, probably largely in terms of quantity and quality of proteins and vitamins, stimulates the ripening of a larger number of Graafian follicles, as well as hastening the onset of estrus. This practice has also been shown in some instances to be effective with sows, although for practical purposes this should be used cautiously with sows, and the cattle or horse breeder is probably better off if his animals do not have multiple births.

It has been shown by Clark that flushing of ewes is more effective in ewes that are not in a high condition to start with and that gain in weight is not necessarily indicative of higher ovulation rates. The preovulatory period is generally lengthened by flushing. McKenzie found that in sows there was a much smaller correlation between gains in weight the 2 weeks previous to breeding and number of pigs farrowed than between gains made the first month following breeding and the numbers farrowed.

Esplin, Madsen, and Phillips have recently reported some interesting observations on the breeding activities of ewe lambs fed on different planes of nutrition during their first winter and previous to breeding. Ewe lambs fed supplemental feeds gained about 25 lb. from October to April, whereas comparable ewe lambs on range gained 10 lb. Both groups were on range from April on and by the following October (when the lambs had become yearlings and were ready for breeding) there was a difference of only 2 or 3 lb. in their weights, the fed ewes being a little heavier. There was a marked difference, however, in the breeding efficiency of the two groups, about 65 per cent of the previously fed ewes giving birth to lambs, whereas only about 45 per cent of those grown entirely on range did so. The special feeding period had ended 6 to 7 months before breeding, and, although it has long been known that flushing ewes just previous to breeding increases fertility,

> . . . an effect on reproductive activity as a result of feeding so long before the breeding season is surprising, particularly since the extra weight advantage gained during the feeding period had practically disappeared by the time of breeding.
>
> This effect may be the result of better development of the reproductive tract at an early age in the lot-fed lambs, thus enabling a higher proportion of them to reproduce at two years of age. It may also be owing to greater storage of some

essential element or elements in the body which are not available in sufficient amounts in range forage, and may be carried over to make possible greater reproductive activity. It is possible that both of these factors may have contributed to the results. This presents an interesting physiological problem, and one of great practical importance, upon which further work is being undertaken.[1]

Certain of the minerals, *viz.*, calcium, phosphorus, and manganese, have been claimed at various times to be limiting factors in reproduction. These claims in general are not justified, for deficiencies of these elements are generally accompanied by other deficiencies such as poor quality of

FIG. 54.—The cow (above) was fed a balanced ration made up of wheat straw, wheat meal, and wheat gluten in 1907. She was in poor condition and gave birth prematurely to the calf (below), which died. In this ration energy and proteins are taken care of, minerals and vitamins are deficient. (*Courtesy of Wis. Agr. Exp. Sta.*)

proteins, lowered palatability, and therefore lowered feed intake, etc. Little of a definite nature is known about the role of the various minerals in normal reproduction. It would not be surprising if later experimental work were to show that the complete exclusion of some one or several of the mineral ingredients had a severely limiting effect on reproduction in the larger animals. However, rations including good proteins will generally automatically have sufficient phosphorus, and those including legumes will automatically have sufficient calcium. If breeders want to play safe by adding a more or less complete mineral supplement to the

[1] ESPLIN, A. C., MADSEN, M. A., PHILLIPS, R. W., Effects of Feeding Ewe Lambs during Their First Winter, *Utah Agr. Expt. Sta. Bull.* **292**, p. 11, **1940.**

ration, it will probably do no harm, but care should be taken that (1) other more likely causes of sterility or lowered breeding efficiency are not overlooked and (2) that these materials of questionable worth are not purchased at too high a price.

The role of the vitamins in spermatogenesis and ovogenesis was discussed in earlier chapters. In addition to its eventual harmful effect on the production of viable sperms and eggs, a vitamin A deficiency has been shown to have a harmful effect on normal gestation and embryonic development, often manifested in abortion or the production of weak

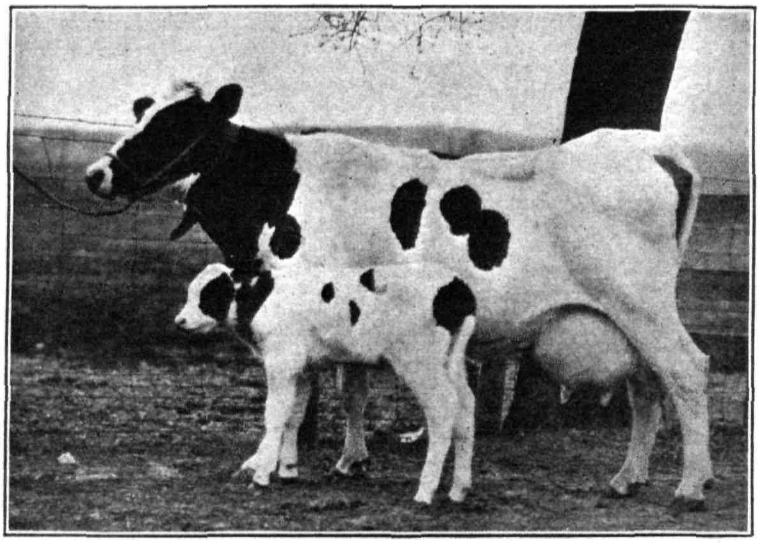

FIG. 55.—This cow was fed the same sort of ration in 1924 as the cow shown in Fig. 54 but got in addition 2 per cent bone meal and 2 per cent raw cod-liver oil. The results are apparent. (*Courtesy of Wis. Agr. Exp. Sta.*)

or dead young in the cow and ewe as well as in rats. There is no evidence, however, that amounts of vitamin A larger than those necessary for normal growth are required for normal reproduction.

Other than its effect on general health, which may of course eventually be reflected in the reproductive system, there is no evidence that a lack of any of the vitamin B complexes have a direct effect on reproduction in the larger mammals. Since the common feeds used for livestock feeding have ample amounts of vitamin B, it would seem to play but a minor role in breeding difficulties in farm animals.

Vitamin C, which can probably be synthesized by all farm animals (an extraneous source being required for only the guinea pig, monkey, and man) was not considered to be a limiting factor in reproduction until the recent work by Phillips *et al.* at Wisconsin. Its injection into the blood stream of slow-breeding and partially sterile bulls was there shown

to be effective in improving the quantity and quality of semen, whereas oral administration proved ineffective. The place of this vitamin in reproduction is still very much in the experimental stage, but the results thus far obtained with bovine males show much promise. Its use may be found to be very helpful in stimulating sluggish reproductive tracts.

There is at present no evidence of any special requirement of vitamin D for normal reproduction, though its necessity for normal growth of the newborn should not be overlooked.

Since vitamin E is apparently so widespread in natural foods and feeds and since no known natural deficiency of vitamin E has ever been reported, it would seem that the livestock breeder could well devote his worries to other more tangible things. The evidence for the efficacy of vitamin E therapy in cattle is not definitely established, and, until more critical experimental work has been done, it would seem wise to reserve judgment as to its definite effect or extraneous necessity in the larger animals.[1]

It will be seen from the above discussion that there is no known special dietary factor or factors involved in the matter of fertility. For the normal expression of this physiological activity our animals surely need to be well-fed. They must have sufficient energy, proteins, minerals, and vitamins, but, if they get sufficient amounts of these ingredients for normal growth and adult maintenance, there is apparently no added requirement of any of them for normal reproduction except those necessary for normal development of the fetus. Certainly there are no known "cure-alls" in the field of nutrition, and breeders should be particularly careful that their attention be not diverted from real problems of a bacteriological nature through flowery claims of this or that panacea.

Domestication has enormously increased the fertility of many species of animals. How much of this change is genetic and how much nutritional and environmental cannot be accurately determined. The genetic powers were evidently present and waited but for better and more abundant nutriment to call them into being. Man himself took a million years more or less to number 750 million in 1800. In the last 140 years he has increased in numbers to over 2 billion, largely because the commercial, industrial, and agricultural (farm machinery) revolutions provided him with more food. Adequate nutrition, therefore, both in the large and in the individual case, is the necessary concomitant of normal reproduction.

Finally, we wish to call attention to the very close relation between fertility in animals and fertility in soils. A recent paper by Albrecht[2] of

[1] See THOMAS, B. H., and CANNON, C. Y., Reproduction on Rations Free from Vitamin E, *Amer. Soc. Anim. Prod. Proc.*, 1937, pp. 59–63.

[2] ALBRECHT, WILLIAM A., Good Horses Require Good Soils, *Booklet* 256, *Amer. Horse and Mule Assoc.*, Union Stock Yards, Chicago.

the Missouri Agricultural Experiment Station discusses this question in relation to horses in a very interesting and enlightening manner. The following things among others are pointed out in this bulletin: (1) the *fallacy of measuring forage in tonnage and neglecting its composition*; (2) the fact that poor soils produce poor plants especially from the mineral-content standpoint; (3) the relation to soil deficiencies of such diseases as pregnancy disease in sheep, acetonemia in cattle, aphosphorosis, osteomalacia, osteophagia, and various ophthalmias; (4) the relation between good soils which will grow legumes with their increased amounts of proteins and minerals and general health in livestock; (5) the relation of heavy rainfall to depletion of soil minerals; (6) the instinctive balancing of rations by wild animals to include the elements their bodies need and the same tendency in domestic animals as evidenced by their choice of feeds which have been grown on soils fortified by the addition of lime and phosphorus; (7) the fallacy of attempting the short cut of adding mineral supplements to forage of poor quality rather than using the longer and surer method of applying minerals to the soil so that they will automatically be found in the crops grown on such soil; (8) the fact that good health for man or beast lies very close to good, fertile soil.

Just as soil fertility and animal fertility are closely related so are general health and breeding health. For the full expression of the inherent fertility that our animals possess, we must supply adequate rations containing all the necessary ingredients, and the more naturally this can be supplied the better. This means, principally, good pasture and good roughage grown on soils containing the necessary elements with the roughage cured and stored in such a manner as to preserve its goodness. If we feed the soil, soil products will adequately feed our animals.

Diagnosis of Pregnancy.—The following are indications of pregnancy in animals: (1) cessation of heat periods, though in some instances animals that have not conceived fail to exhibit further estrual periods and also some that have conceived do exhibit estrus during pregnancy, probably, as Williams suggests, because of the atrophy of the corpus luteum; (2) formation of the characteristic adhesive uterine seal in the cervix; (3) presence of normal corpus luteum in the ovary; (4) increased size and functional activity of the uterine arteries; (5) palpation of the uterus (or horns) per rectum showing it to be firm, tense, and fluctuating; (6) increased size of the female; (7) auscultation of fetal heart; (8) movements of the fetus; (9) general tendency of females that have conceived to become more quiet and to lay on flesh. It is possible late in gestation to feel the fetus at the base of the right flank.

Laboratory tests have been devised for the determination of pregnancy. These are based on the different levels of hormones found in the blood and urine of pregnant females. In the human the Friedman

modification of the Ascheim-Zondek test is the one most generally used. It is based on the greatly increased amount of anterior pituitarylike substance found in the urine of pregnant women. The procedure consists of injecting 7 to 10 cc. of morning urine into a mature female rabbit's ear veins at two 12- to 15-hour intervals. The rabbit is then killed at the end of 48 hours and the ovaries removed for examination. The presence of subserous hemorrhagic areas or corpora lutea constitutes a positive reaction, whereas clear retention follicles with no hemorrhagic areas are signs of a negative reaction. This test is positive, in cases of pregnancy, 3 or 4 days after the expected date of the first missed menstrual period. Since estrin is also produced in increased amounts during pregnancy, its presence in urine, as determined by estrual changes in the vaginal smears from rats, is also used to determine pregnancy.

In the mare, pregnancy may be detected from the fortieth to one-hundredth days of gestation by injecting the mare's serum into immature female rats. A positive reaction is manifest by increased size and activity of the rat ovaries and uterus because of the increased gonadotropic hormone in the blood of pregnant mares. From the one-hundredth day of pregnancy until term, sufficiently large amounts of estrogens are present in mare's urine to cause castrate female rats to exhibit estrus or spayed mice to show certain vaginal changes when injected with urine of the pregnant mare.

Clinical Examination of Male Genital Organs.—In estimating probable fertility it becomes necessary to examine the reproductive organs. In the male this is somewhat more easily accomplished than in the female. With the stallion or bull, it is best done with the animal in a standing position, but in all cases precautions concerning safety must be taken. The stocks are often used to confine stallions, whereas the bull can be handled in the stanchion with a rope fastened around one leg above the fetlock, passed around the other leg, and the loose end held. When the animal is restrained, the testicles can be examined from behind.

There should be two, of approximately equal size, of a firm, tense structure and even contour, and they should show no evidence of heat, pain, or swelling. The epididymi and part of the vasa deferentia can also be examined from this position, particular attention being given to the tail or lower portion of the epididymi, where infection often lodges. Per rectum, the vasa deferentia can be picked up as they emerge from the inguinal canal and followed along to the vesiculae seminales, prostate, and Cowper's glands.

To examine the bull's penis, he is usually thrown on his side, and his feet stretched out front and back and secured with ropes to stout posts. In this position the sigmoid flexure of the penis can be eliminated by pushing forward and upward and the glans protruded from the sheath.

Moderate traction will bring the penis into view when the retractor muscle has become fatigued, and the organ can then be examined for any abnormal conditions. The penis of the stallion can be brought into view by inserting the hand in the sheath, grasping the penis behind the glans and exerting moderate traction until the retractor muscle becomes fatigued.

To complete the examination, it is necessary to secure and examine a sample of semen as described in the chapter on artificial insemination. It should be of sufficient volume, milky white, and viscid, and, when examined under the microscope, exhibit closely packed fields of normally formed and active spermatozoa. The copulatory act itself should be watched closely to see that it is performed eagerly, completely, and without evidence of pain.

Clinical Examination of Female Genital Organs.—It is entirely possible and often necessary for the veterinarian or trained herdsman to examine carefully the structure and condition of the female genital organs of the mare or the cow. As in examining the male, it is first necessary to place the animal in an entirely controllable position from which no injury is likely to arise either to operator or animal. When this has been accomplished, the vagina and vaginal end of the cervix can be examined by carefully inserting the hand. The nails should be cut back short, and the hand thoroughly cleaned and fingers placed in a cone shape. Forceps can be attached to the cervix and gentle traction exerted pulling it back into view.

Physiologically, the vagina of the cow at estrum and when nearing parturition contains an abundance of clear, rather fluid, highly lubricant mucus. The vagina of the non-pregnant cow in the interval between estrual periods contains a small amount of lubricant mucus. The vagina of the pregnant cow, except when nearing parturition, contains a highly adhesive mucus. These physiologic variations in quantity and quality of vaginal mucus need to be learned by actual clinical observation before the various pathologic contents may be readily recognized.[1]

Rectal palpation is also extremely valuable in determining an animal's genital health and normality. Such rectal examination, after removal of the feces by hand, usually reveals the cervix, 3 to 5 in. long (cow or mare) on the floor of the pelvic cavity between the bladder and the right pelvic wall. This followed anteriorly leads to the somewhat broader and softer uterus. In cattle the body of the uterus is rather short giving rise anteriorly to the two horns of the uterus. These in the cow proceed forward and upward, then turn down and back forming an almost

[1] WILLIAMS, W. L., "The Diseases of the Genital Organs of Domestic Animals," pp. 87, Andrews and Church, Ithaca, N. Y., 1921.

complete circle. Arising from the end of the horns are the oviducts, often difficult of recognition by rectal palpation. They are about 1/10 in. in diameter, sinuous, smooth, and firm. They pass laterally below and in front of the ovaries, both oviducts and ovaries being embedded in the broad ligament. Lastly the ovaries themselves, situated in the broad ligament, can be palpated. They usually lie close to the inlet of the pelvic cavity near the horns of the uterus.

Examinations such as have been described for male and female, when performed by competently trained and experienced men, are invaluable to the breeder and the expense is small compared with that incurred in maintaining sterile animals over periods of months or years and possibly spreading contamination throughout the herd.

Summary.—We have seen in this chapter that fertility means the ability to produce viable germ cells capable of uniting with germ cells of the opposite sex and resulting in vigorous, living offspring. This manifestation sets in when animals are relatively immature from a physiological standpoint at a time known as *puberty*. Fertility is lacking in newborn animals, manifests itself first at puberty, from which time fertility rises for a time, levels out, and then recedes again with the onset of senility. We have seen that fertility is an inherited characteristic, as are all other characteristics exhibited by animals. It was pointed out that fertility may be directly related to conformation and is greatly affected by management and nutrition. Finally the methods of diagnosing pregnancy were delineated and the procedures in the clinical examination of the male and female genital organs were discussed.

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[1] For books, see lists at ends of Chaps. IV, V, VI.

CHAPTER VIII

REPRODUCTIVE EFFICIENCY

Reproductive efficiency connotes the optimum effective use of the reproductive powers of all the animals in a herd or flock. In the female, it is the regular production of offspring over a period of years; in the male, the successful fertilization of the largest number of eggs with the fewest possible services. Although differing rates of fertility in both males and females may have a genetic basis, nevertheless, differences in reproductive efficiency are for the most part traceable to differences in management and general care. We should never overlook the fact, however, that our animals are individuals and that the best management of one may not necessarily be the best for another. For the most part livestock management entails the application of common sense directed both by previous experience and by a knowledge of scientific principles. The more thoroughly the principles are understood and the greater the accumulation of experience, the more efficient should be the management. Without good judgment or common sense, neither knowledge nor experience, nor both, will avail to render a livestock-breeding enterprise profitable. The question of reproductive efficiency will first be discussed from the standpoint of the male, then from that of the female.

REPRODUCTIVE EFFICIENCY IN MALES

Service for Immature Males.—There is common agreement on the fact that the body, as a whole, should not be used for hard work until mature. Yearling horses are not put at hard work because it is readily realized that, although some immediate service might be secured from an animal so used, in the long run the loss would overbalance the gain through such a procedure. The general growth of a colt so used would be stunted, and it would probably develop some of the common unsoundnesses, such as spavins and ringbones, because its body was subjected to too severe a strain before it had matured and hardened. The same general laws of relative weakness before maturity probably apply as well to the procreative powers of individuals, and a promising young male would probably be injured by allowing him excessive service while young and before the reproductive organs have more fully matured. Just as in the case of the yearling horse, a temporary benefit, in the form of a few offspring, might be derived, yet in the long run these offspring might have

been purchased at a very dear price, because in the process the animal might have been ruined for future breeding service.

Not enough controlled experimental work has as yet been done in this field to allow the drawing of any but the very broadest conclusions, and in the following discussion the writer has tried to err on the conservative side. Even after research has established the general principles of the optimum use of sires, they will need specific interpretation in each individual case.

Stallions.—Stallions should not be used for service until at least two years of age, and at this time only in a very restricted manner. At this age, they can serve a few females only, *i.e.*, one service a week for 8 or 10 weeks during the breeding season with at least a full week's rest between services. With well-grown young stallions, the temptation to use them more often is great, but, because it may result in more or less permanent harm to the animal, it should be avoided. At three years, the stallion can serve two or three times a week for the 12 breeding weeks, or 25 to 40 mares per season. At four years, the amount can be increased to 50 or 60 services, and a mature five-year-old stallion can serve 80 or 90 females during the year. It is sometimes necessary to use mature stallions two or three or four times a day, and occasionally this can be done but should be followed, if possible, by a day or two of rest.

Bulls.—Bulls at one year of age can be used for light service if desired. Here again extreme care and good judgment must be used, and the number of services kept down to 10 or 12, with preferably a rest period of at least a week intervening. At two years of age a bull can serve 25 or 30 females; at three years, 40 or 50; and, after four years, can take care of a herd of 60 to 80 females. The total amount of semen ejaculated by a bull is not large—3 to 4 cc. Bulls, therefore, can be safely used two or three times a day for short periods with adequate rest periods following. Various systems are in vogue in cattle artificial-inseminating associations, a fairly prevalent one being not to use the bull more often than every other day with occasional longer rest periods.

Boars.—Boars, if well-grown, can be started in service at eight or nine months of age, but during their first breeding season they should not serve more than once a week, with a full week's rest between services. At a year, they can be used a little more heavily, *e.g.*, on 15 or 20 sows; at eighteen months, on 25 or 30; and, after two years, can take care of a herd of 40 or 50 sows if necessary. Because the boar ejaculates so much more semen (200 cc.), he generally should not be used in service so frequently. Yearling boars can be used every other day for short periods and mature boars consecutively for 2 or 3 days followed by a day or two of rest.

Rams.—It is seldom advisable to use a ram lamb for service, though this is sometimes done. The safe plan is to keep the ram out of service until he is at least eighteen months of age, which will come during the second fall of his life. At this time, he can be used on 15 or 20 ewes, the following year, at two and one-half years of age, he should be able to serve 30 or 40 females, and after that as many as 80 or 90 if desired. Because the ram ejaculates so little semen at any one service (0.8 cc.) he can be and often is used many times a day during the breeding season. A short rest period seems enough to restore a ram to normal breeding power.

Individuality.—In all of the foregoing discussions relating to the various classes of males, the time and number of services must depend very largely upon the individuality and rate of growth of the individuals concerned. The foregoing are average estimates based on hand coupling of well-grown animals and are purposely pointed toward a conservative, safe practice.

Animals show very great variations in their rates of sperm depletion through service. This is true both among species and among individuals in a given species. They also vary greatly in the time required to return to normal following heavy service. The only way to determine how much usage a male can stand is by actual trial. Any male can be used up to the point where the quality or quantity of the ejaculate begins to decline, and this will probably be somewhat variable between individuals, as well as influenced by general care, season of the year, etc. A really good breeding male is invaluable, and his health—especially breeding health—should be carefully conserved. When we have a really good male, we should use him as much as possible, consistent with his ability to impregnate females over a long period of years. The breeding efficiency of poor sires should be conserved by not using them at all.

There has never been shown to be any definite correlation between masculine type or sexual desire and the presence of copious amounts of semen and numbers of viable spermatozoa, but, on the other hand, there are records of sterile males that serve vigorously and often if given the opportunity.

Males should be trained in so far as possible to perform their breeding work according to certain definite routines as to general handling, exercise, time of serving, place of serving, etc. They should not be allowed to serve immediately following a heavy meal. If it should become necessary to have a stallion, bull, or boar serve twice during one day, it is well to arrange the services as far apart in the day as convenient.

First Service.—Good judgment should be used in seeing that an animal's first attempt at service is successful. Young males of any class may be seriously injured through carelessness in letting them serve vicious

or nervous females, or without due precautions having been taken to see that the young, inexperienced male is not subjected to unnecessary risk. With stallions, this is particularly important, and under these conditions, if not always, strong hobbles should be used on a mare. As an example of the harm that may result from carelessness at this time Anderson cites the following case:

A Thoroughbred Stallion—When this stallion was observed he was beginning the second season in the stud. He had been mated to thirty mares the previous season and only one proved to be in foal.

The statement was made to us by his owner that in making one of his first services he fell and severely injured a vertebra of his tail. After this injury he did not, it was reported, serve close. He would barely enter and discharge close to the vulva.

When he was allowed to serve a mare in our presence the story told of his service the previous season was confirmed. He had formed the habit of entering but a short distance, discharging, and, of course, drawing out the discharge as he came down. The semen was found to be without fault. The barren mares, a great loss to the farm, were caused by his not giving a better service. Semen deposited just within the lips of the vagina will be wasted on the withdrawal. Frequently stallions are guilty of this fault, and when it happens the service should not be counted but the mare remated.[1]

If there is a great discrepancy in size or weight, a breeding crate or rack should be used in order to facilitate service and to establish the young male's confidence in himself. Rough, uneven, or stony ground should be avoided as a place for service, for obvious reasons. It is good practice with any class of animals to reserve a certain place for actual service, and this should in no case be the stall or pen of the male, as such practice is very apt to lead to the development of the habit of masturbation in the male. Such a breeding pen should be out of sight and out of contact with the rest of the herd. It should be kept clean and constructed so as to avoid all possibility of accidents.

One Service Sufficient.—Reproductive efficiency implies that the best possible use is to be made of the breeding powers of all the animals concerned. In the case of the male, this immediately rules out the practice of allowing a male to serve a female more than once at a given time except as noted with mares, though here two services are not usually allowed on the same day. If the first service is complete in every way, a second service is superfluous. It is a wasteful practice as far as the male is concerned. At each service where ejaculation occurs within the female organs, there are deposited from 1 to 30 billion or more spermatozoa. Only one spermatozoon functions in fertilizing an ovum, so that if none

[1] ANDERSON, W. S., Sterility in Relation to Animal Breeding, *Ky. Agr. Expt. Sta. Res. Bul.* 244, 210 pp. ,1922.

of the billions of spermatozoa of the first service, provided it is a complete, satisfactory service, can fertilize the ovum, it is futile to expect that any of the second might accomplish this result. Mere numbers are amply supplied at the first service, no number of further services at this time will make fertilization any more probable, and the continued excitement may cause the female to expel all the spermatozoa that have been deposited by previous services. Discussing this point in horses Anderson says:

> The fact remains, however, that a very great percentage of barrenness in mares is not due to disease or disorders but to the highly artificial method of mating horses. If a band of brood mares are turned into the pasture with a potent stallion, he will have foals by close to 90 per cent of them. Our best breeders rarely exceed 50 or 60 per cent. In the pastures the stallion will mate with each mare many times during one heat period, while under control a mare rarely gets more than one service. One would be sufficient were it made at the right time with reference to the liberation of the egg.
>
> There can be no doubt that the time of the shedding of the egg varies with the individual mares, the same mare, perhaps, behaving differently at different times. Assuming that such is the case, it is hopeless to expect a solution of the problem as long as the present method of breeding is employed.
>
> The universal custom of horse breeders is to mate a brood mare, if she does well at foaling time, on the seventh, eighth, or ninth day after dropping a foal. Most breeders prefer the eighth day if the services of the stallion can be secured on that day. Experience shows that this time after foaling is the right time in which to get the greatest number of pregnancies. If it were possible to give two services to a mare with foal at side, in order to double the chance of obtaining pregnancy, they should be given on the eighth and tenth days, or seventh and ninth.[1]

Recent experience of numerous investigators indicates that foal heat is not the best time to breed. The second and third heat periods are probably best, for involution of the uterine mucosa is often incomplete at foal heat, and a greater percentage of pregnancies can be secured during the second and third heat periods.

If a male has not been allowed or had occasion to serve a female for several weeks, it might be wise to allow him to serve twice, for the sperm ejaculated at the first service might be old and not of good quality.

The usefulness of really high-class sires can be extended through the use of "teaser" males. The usual practice in using teaser males is to tie or strap a weighted apron in front of the sheath or to use vasectomized males. These males when turned out with a group of females will discover those that are in heat, they can then be removed, and hand coupling with the more valuable sire resorted to. In this way it is possible both to

[1] *Ibid.*, pp. 225–226, 1922.

conserve the vitality and to extend the usefulness of the really superior sire.

Results of Excessive Service.—The effects of excessively numerous services by males of many species have been reported. Lode (1891) was apparently the first to study this problem. His work was with dogs and showed a sharp decrease in number of spermatozoa with frequent successive copulations. If the intervals between services were 48 hours or longer, the decrease was not great. Hays (1918), working with rabbits, reported that excessive service by male rabbits reduced the fertilizing power of semen and that certainty of pregnancy declined, although the pregnancies which resulted under heavy service of the male were as large and healthy and grew as fast as others produced under lesser service. Hammond (1921) found, however, that 39 services by a male rabbit in 8 hours did not reduce fertility.

Lewis found that one stallion produced 65 cc. of semen containing 131,000 spermatozoa per cubic millimeter at the first service, and during 9 successive days, on which the stallion served once each day, the amount of semen and number of spermatozoa declined steadily so that the service on the ninth day produced only 5 cc. of semen and about 6,000 spermatozoa per cubic millimeter. In another stallion the number was reduced from 232,000 to 43,000 spermatozoa per cubic millimeter over a period of 10 days during which one service was allowed daily.

Bulls differ somewhat from stallions and boars. Milowanow (1934) explained this on the basis of the differences in anatomical structure of the sex organs. In species like cattle and sheep the male genital organs are constructed in such a way that they can breed frequently. They produce comparatively small amounts of semen of high sperm concentration, for their accessory glands are of small volume and add only minute amounts of fluid to each ejaculate. The duration of copulation is very short in these species, and a small amount of semen containing many sperm in highly concentrated form is ejaculated. Consequently, the storing organs cannot be depleted of all semen by one ejaculate. Many experiments at Russian breeding stations have proved the correctness of this assumption. Kirillow and Morosow (1933) found it difficult to produce complete exhaustion of spermatozoa in bulls through frequent matings. They studied the mating capacity of ten bulls and observed on one occasion that one bull made twenty-four ejaculations in twenty-seven hours, the last ejaculate still containing live sperm in good concentration. The concentration was maintained at the same level (348,000 per mm) for the first fifteen matings, then dropped sharply. Eighteen hours, rest restored normal concentration in the next ejaculates. In another experiment nine bulls were each allowed to breed eleven times in one day. The average total number of spermatozoa per ejaculate dropped from 240 millions to 216 millions in the sixth ejaculate; by the tenth ejaculate the original number was again reached; and the eleventh still contained 160 millions. If bulls were allowed to serve one, two, or three times daily, those making three serv-

ices daily produced the largest volume and the best semen of the three groups. These investigators also claimed a beneficial effect on the quantity and quality of the ejaculate if the bull spent some time getting ready to mount. Energetic bulls with strong sexual impulse ejaculated smaller amounts of semen than less active bulls. The second ejaculate was often of higher quality than the first. They concluded that bulls produced sperm continuously and regenerated a supply in less than twenty-four hours and that mating stimulated sperm production through neuro-psychic connections. After more recent experiments, Kirillow (1935) suggested that for prolonged use two matings daily would be the optimum number. A group of bulls giving three daily services showed signs of decreased sexual potency. Lagerlöf (1935) reported observations similar to those of Kirillow (1933) on the influence of number of matings on sperm content. He let a bull serve twenty-nine times on nineteen consecutive days. Although the number of spermatozoa was decreased in some ejaculates (no actual numbers were given), a rest period of one night was sufficient to restore the normal number on the following day. Often the second and third ejaculates contained more spermatozoa than the first, especially if the bull served at intervals of only a few minutes, which also agreed with Kirillow's observations on the influence of sexual excitement.[1]

McKenzie and Berliner[1] (1937) in an extended study of mating ability in the ram report: (1) great variability in breeding activity between individual rams up to five services in 10 minutes; (2) variability in amount of semen ejaculated from a few tenths of a cubic centimeter up to 1.5 cc. with volume not appreciably affected by frequency of service; (3) a steady decrease in number of spermatozoa after the first or the first few services leading finally in some cases to services without emission; (4) the production of abnormal morphological sperms in the case of only one ram. Neither motility nor viability of the spermatozoa was given extended study. They conclude that complete exhaustion of sperms in the ram is hard to obtain and that a short rest period suffices to restore spermatozoa depleted by excessive service.

McKenzie, Miller, and Bauguess (1938) have studied the effect of the frequency of ejaculation on the quality and quantity of semen from normal boars. They found: (1) that variability among individual boars was considerable; (2) that the amount of semen was not reduced by services at 48-hour intervals, was reduced in one boar at 24-hour intervals, and in all the boars by only 12-hour intervals between services, although the smallest boar in the group yielded an average of 313 cc. of semen in 18 ejaculations spread over only 14 days; (3) that there was no correlation between live weight and amount of semen per ejaculate in the boars studied; (4) that the average sperm concentration per cubic millimeter was about 100,000 at services not closer together than 24 hours and

[1] McKenzie, F. F., and Berliner, V., The Reproductive Capacity of Rams, *Mo. Agr. Expt. Sta. Res. Bul.* 265, pp. 41–42, 1937.

dropped to about 50,000 per cubic millimeter at the third service when they were allowed at 12-hour intervals; (5) that the total number of sperm ejaculated at the first service ranged from 26.8 to 76.8 billions, averaging 20 billion or more per day over a 14-day period, remaining fairly constant at services not closer than at 48-hour intervals, but dropping appreciably after 3 or 4 days on a 24-hour service basis and still further when services were allowed at 12-hour intervals; (6) that the spermatozoa retained motility for 8.5 days on a 72-hour service schedule, 4.6 days on a 48-hour schedule, 3.5 days on a 24-hour schedule, and 2.5 days on a 12-hour schedule; and (7) that the number of abnormal sperms per 1,000 tended to increase somewhat with more frequent service, being particularly marked in the 12-hour schedule and showing a consistent relation between the abnormality count and the duration of sperm motility.

All the above data suggest that, although our breeding males are generally gifted with tremendous powers of sperm production and are capable of carrying on excessively high rates of mating for short periods, nevertheless, these powers have limits, especially in younger animals, which it will be wise for the breeder not to try to approach too closely.

Here in particular it is best to try to approximate the happy medium between too little and too much service. And a further angle of this happy-medium idea is that males probably breed best and most surely under regular service rather than under a system which calls for too much service for a short period followed by a long period of inactivity.

General Management of Males.—Because the breeding efficiency of the male, from a purely physiological standpoint, to say nothing of his influence from a genetic standpoint, can and does contribute so much to the economic welfare or otherwise of his owner, it would seem that the question merits a lot more attention than it often gets. All too often, males are poorly housed and get only the leavings as far as feed is concerned and nothing that could be dignified by the word *care*.

We have discussed the matter of exercise in the chapter on fertility. The best breeding condition for males is described as that of being in a lean, hard condition. Without suitable and sufficient exercise, this is not often possible of achievement. Stallions, bulls, rams, and boars should at all times be provided with suitable shelter, have access to a good-sized yard with summer grazing and are generally better off with another animal or two for companionship.

The feed for breeding males should be complete from a nutritional standpoint and, of course, should be palatable. An additional amount of protein, especially from animal sources, can well be fed just previous to and during the heaviest portion of the breeding season. Males cannot perform their essential function in a satisfactory manner if they must subsist largely on a poor roughage ration that leads to overdistention of the

alimentary tract and general sluggishness. Good feeds are needed at all times, but it is generally unwise to pin one's faith on various and sundry vitamin or mineral mixtures, at least until experiment has proved their need and efficacy.

Berliner, Cowart, and Pharis have recently demonstrated the advantages of a mixed ration of oats, wheat, and bran over corn alone as a feed for breeding jacks and stallions. The mixed ration increased the volume of semen as well as the sperm concentration and the keeping qualities of the semen. The Bureau of Dairy Industry of the U.S. Department of Agriculture has for many years been feeding sprouted

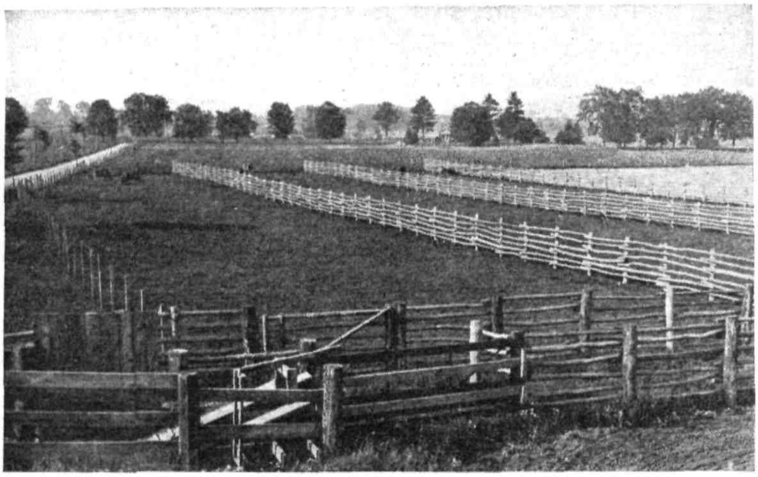

FIG. 56.—Exercising paddocks for bulls at Massachusetts State College Farm. It is essential that old bulls secure sufficient exercise.

oats to their breeding bulls with a resultant rise in breeding efficiency, especially marked in older bulls.

Good feed and care of breeding males is receiving increasing attention under the stimulus of artificial insemination. If an association is to breed successfully 1,000 or 2,000 cows artificially to some particularly good bull each year, the matter of semen production by the bull demands, and is getting, some attention. Long ago we learned how to increase milk production in cows by improving their feed and care. We now face the same problem in semen production by males, and it will probably be solved in much the same fashion. There is a possibility that vitamin E and anterior-lobe hormone may prove useful in this regard.

Not a great deal is now known about equine, bovine, ovine, or porcine psychology. We have known for some time that certain animals did not mate readily, that moving sires to new locations was often followed

by long or short periods of sterility. The underlying causes are not yet well understood, but they merit careful thought and experimentation. We have long known that males not trained to use a breeding rack in early life are often taught with great difficulty, if at all, in later life. Now, in artificial-inseminating work, we are running into much the same problem of males refusing to serve while an attendant stands close by with an artificial vagina ready for use. Our highly bred animals are rather delicately balanced organisms from a nervous standpoint, and we have much to learn along these lines before we can get 100 per cent service (in the general sense of that term) from them.

Our males generally serve eagerly when young if conditions are made suitable. Our task is to retain that quality in them as long as we desire to use them. We know too, contrary to some rather extensive opinion, that genetically a male will transmit the same at any age—one or twenty—that the genes do not change with age, experience, production, or any other extraneous influences.

Males should be purchased subject to their ability, willingness, and success in impregnating sound, healthy females. It would probably be wise also before laying down a good price for a breeding male to have a veterinarian examine his semen, because what we are really buying when we purchase a male is semen containing viable germ cells, and these in turn contain, we hope, the genes that will bring about improvement in our herd or flock. For some types of genital diseases the only way to tell if a male is diseased is through using him. Preferably a male should be bred to a limited number of females and then held out of service for a few weeks to see if gestation is proceeding normally.

Besides making the external conditions conducive to the success of a young male's first service, strict attention should also be given to the internal conditions of the female genital tract. If, as should always be the case, the young male has come from healthy parents, has grown up in a clean environment, and has been furnished suitable feed, he should reach puberty strong and uninfected. If this is true one cannot be too careful in guarding him against infection. The male should be examined by a competent veterinarian and, if judged sound, is ready for service. He should be allowed to serve only healthy females. The pernicious practice of allowing healthy young males to serve females that have been unable to conceive from one or several previous services cannot be condemned too severely, though it is often practiced even when the female has a purulent discharge. Infection is all too prevalent and must be guarded against continually. A clean herd can be had if due care is exercised, and, when this end is once attained, its health should be guarded diligently in every detail.

Over a period of years your sires will make or break you, so

1. Select them intelligently.
2. Treat them understandingly.

A male can only transmit a sample half of what he got from his parents. If he does not sire good offspring, don't blame him, for the blame actually rests on you or whatever breeder bred his sire and dam and mated them.

REPRODUCTIVE EFFICIENCY IN FEMALES

When to Breed Females.—This question was discussed somewhat in the chapter on fertility. The normal time of puberty in all our farm animals is known, though females should not necessarily or generally

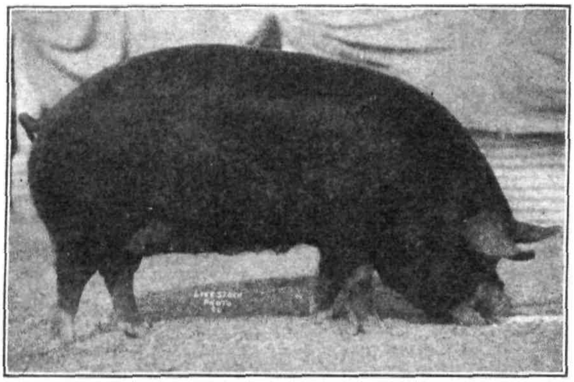

FIG. 57.—Baron's Helen 2nd, a sow which raised two litters of pigs in 1924 as well as being made Grand Champion Berkshire Sow at the National Swine Show. She was reserve Grand Champion in 1925.

be bred at the time that this first becomes possible. Some females are undoubtedly bred before it is wise. Others undoubtedly are left virgin too long. Until a breeding female is at work in reproduction, she is a daily financial burden, and only when she begins to reproduce does she stand any chance of returning a profit. Our aim, therefore, should be that of getting our females at their job of reproducing at as early an age as is consistent with their own health, ultimate size, and efficiency. McKenzie[1] has shown that sows bred to farrow first at eleven months and continuously thereafter will reach a mature weight equal to sows bred first at eighteen months or two years. Gestation neither retarded nor speeded up growth, but heavy lactation did retard growth temporarily.

Bogart, Sperling, Barnes, and Asdell[2] have shown: (1) that castrated female rats grew faster than bred or virgin rats; (2) that rats bred at

[1] McKENZIE, F. F., Growth and Reproduction in Swine, *Mo. Agr. Expt. Sta. Res. Bull.* 118, 1928.

[2] BOGART, R., SPERLING, G., BARNES, L. L., and ASDELL, S. A., The Influence of Reproductive Condition upon Growth in the Female Rat, *Amer. Jour. Physiol.* **40**: 355.

normal age and their young killed immediately so that they were pregnant most of the time but not lactating grew more rapidly and for a much longer time than virgins or those bred early or late; (3) that early bred and lactating females were somewhat retarded in growth due to lactation but that they eventually reached the same adult size as those bred later; (4) rats bred at normal age (about 100 days and somewhat after puberty) grew most rapidly next to the castrates and those bred at normal age with young killed, and eventually reached the greatest weight; (5) that rats bred late were retarded in growth and did not reach the weights attained by castrates, those bred early, or at the normal time; (6) that virgin rats were most retarded in growth and attained the smallest size at maturity.

Pregnancy, therefore, seems to be a stimulus to growth perhaps because the estrogens affect the activity of the pituitary gland. Heavy lactation in early life, on the other hand, retards but does not destroy the growth impulse.

Females should, therefore, be bred moderately early although too early breeding and, even more, too late breeding should be avoided.

Measurement of Breeding Efficiency.—In range cattle and in sheep, breeding efficiency is generally measured in percentage of calf or lamb crops. For full efficiency in the former, it should be 100 per cent (which it seldom or never is), and in the latter something over 100 per cent, due to at least a few multiple births. In the dairy cow, breeding efficiency can be measured by the average time elapsing between calving and the next successful breeding. If a herd of dairy cows is successfully impregnated within 90 days following calving they will freshen at about yearly intervals and would score 100 per cent in this regard. In most herds, however, the figure is probably nearer to 140 or 150 days between calving and the next successful breeding. In hogs, breeding efficiency is perhaps best measured by the number of pigs weaned per sow rather than those farrowed. If sows weaned 7 pigs in one litter or 12 or 13 in two litters, they would be better than average and should perhaps rate near 100 per cent in this regard. In mares, the number of foals dropped and raised divided by the number of mares bred will give a good measure of breeding efficiency.

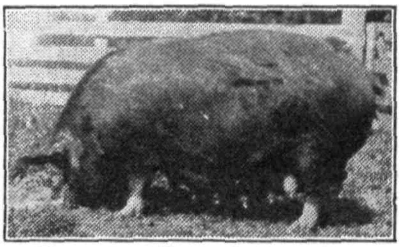

FIG. 58.—Silbirfa Duchess 15th, a Berkshire sow which farrowed 18 litters totaling 172 pigs. The eighteenth litter was farrowed when the sow was 10½ years old. (*Courtesy American Berkshire Association.*)

In addition to actual numbers born and/or raised, some attention should also be given to the vitality and general type of the young produced

and their ability to withstand diseases and setbacks, so common in young animals, and to survive and grow rapidly and efficiently into desirable animals.

Records That Help Breeding Efficiency.—Someone has remarked that "the least used tool on the average farm is the lead pencil." Others state that "you can't breed good livestock with a pencil." It is true that nature provided other means for the actual breeding, but it is also true that no breeder is likely to make a great success of breeding unless he uses a lead pencil.

The breeder should keep accurate and complete records of the breeding efficiency, health, and general accomplishments of all the animals in his herd. It is especially important that he keep a record of heat periods. Many breeders fail to do this and suddenly find themselves in a morass of breeding difficulties with the breeding program badly out of balance. In cattle, for instance, the cows should come in heat about every 19 to 21 days if they are normal. If the breeder finds from his records that certain cows are coming in heat at 19 days, then at 34 days, then at 14 days, etc., he can immediately conclude that something is wrong and with the veterinarian's help straighten things up before the breeding program has been entirely wrecked.

Birth weights of calves, colts, lambs, and pigs should be recorded as well as their weights at stated times, such as at two months, at weaning, at six months, etc.

Type and quality of each offspring should be set down and compared with similar figures for the dams. It is only in this manner that a breeder can get a true picture of what each sire and dam is actually accomplishing in his herd. The first prerequisite for a breeder is that he have a definite goal, and he must keep records to check his progress toward it.

The number of services required per conception will give a general notion of the over-all breeding health of his herd or flock.

Breeding better livestock is a difficult matter at best, and without recorded data to serve as guideposts the breeder is more than likely to flounder, having no accurate knowledge of the breeding efficiency of his animals and no recorded factual data on which to base his selection.

General Management of Females.—From the standpoint of breeding efficiency, the females should of course have been selected from naturally fertile strains. In this regard it seems advisable to call attention to the much greater worth of lifetime over partial aspects of fertility. A sow may have one or two large litters of vigorous pigs and several small ones of weak pigs. One or two separate outstanding accomplishments in breeding efficiency should not be allowed to obscure the general average. The intelligent breeder realizes that often his best sows which have milked the heaviest are the poorest looking at weaning when the sows are often

culled. Likewise twin lambs often compare somewhat unfavorably in size and appearance with singles, but the former are more likely to have a higher degree of inherent fertility.

Females of any species are quite likely to be born healthy, our task being that of seeing to it that they do not lose this original state.

Reproductive efficiency in the female is perhaps even more difficult to maintain than in the male. The female genital tract presents a relatively larger surface that may become infected, as well as more favorable places for bacteria to lurk. The ovaries themselves may be diseased or covered with cysts, and they are more difficult to examine than the testicles in the male. A complete examination of the female genital tract is possible at least in mares and cows and may be given periodically in order to detect the first indications of trouble. An excellent place for disease to lurk is in the small convoluted Fallopian tubes leading from the ovaries to the uterus, this trouble being known as *salpingitis*. Farther down, the horns of the uterus or the body of the uterus may be infected, giving rise to various forms of metritis often accompanied by a discharge of pus. The narrow, contracted cervix, or neck of the uterus, may be the seat of infection. Infection may also lurk or an unfavorable condition be present in the vagina, and in either case the spermatozoa deposited by the male might be destroyed.

Many a breeder has paid dearly for his carelessness in bringing diseased females into a clean herd. In any purchase of new breeding stock the consideration of both general and genital health must take first rank. In general it probably would be better and more profitable in the long run to get poorer genes in a healthy body than better genes in a diseased body. Disease, if it comes gratis, is expensive. Certainly we cannot afford actually to pay cash for it.

Most of our females must do double duty; *i.e.*, they must produce and reproduce. The breeder's task is to strike a balance between these. If one is overdone, the other is quite likely to suffer. Our general-management practices should be aimed to keep our animals as close to nature as possible. Dairy cattle have probably been bred and selected further away from their natural state than any other class of animals, and this no doubt largely accounts for the fact that greater breeding difficulties are encountered with this class of stock than with any of the others. Here again the ideal is the happy medium between pampering and too much harshness.

Feeding the breeding female so that she can both produce and reproduce at the optimum rate in both fields calls for knowledge and judgment. If an animal is getting what it needs for normal growth and production, no additional kind of feed is necessary for normal reproduction. Balanced grain mixtures, good-quality roughages, and good pastures will take care

of both production and reproduction without the addition of various expensive cure-alls and panaceas.

It is well known that both males and females perform best if they are in a gaining condition just previous to and through the breeding season. Such management is more conducive to the optimum functioning of the reproductive tracts than one in which the animals are kept in a stationary or a falling condition. Excessive fatness, with its usually attendant lethargy, or such poor condition that there is barely enough nourishment for the normal functioning of the bodily mechanisms concerned with survival and nothing left over for the reproductive function will, of course, result in lowered breeding efficiency.

Good breeding females, like males, are none too plentiful. When we get them, we should so plan our management that we may retain them in the herd or flock as long as possible. In so doing we (1) spread their original cost over a longer period of years, (2) get more offspring from them, and (3) are able to select more intensively because the herd is not turning over so rapidly.

To keep animals in a normal condition of productive and reproductive health is difficult. It requires knowledge, care, intelligence, record keeping, and good judgment.

To restore animals to health when once they become weakened, inactive, or diseased is a very difficult and sometimes impossible task.

It would probably be cheaper for you to pay your veterinarian to keep your herd in a healthy breeding state than to send him an S.O.S. after things get awfully bad, and it would certainly be better from the standpoint of the animals.

Probably most variations in reproductive efficiency are due to management or to failure to understand the normal processes. If your herd or flock is not in a high state of reproductive health, it is more likely to be your fault than theirs, so:

1. Check your general feeding and management practices.
2. Don't waste time and money on cure-alls and panaceas.
3. Don't delay too long in getting the help of your veterinarian.

Breeder and Veterinarian Relations.—There are three possible points of view concerning the relations between breeders and veterinarians. One of these is that the veterinarian should be called to take care of every departure from normality in animals as regards health (or accident) no matter how slight. The other extreme is that an experienced herdsman can entirely dispense with the services of veterinarians and diagnose and treat all health abnormalities in his herd or flock. The writer thinks that both extremes are wrong and that there is a middle ground, somewhat variable between individuals, which is better for all concerned. If a cow scratches her udder or steps on a teat or a colt cuts himself on a barbed-

wire fence, an avenue of infection is opened up that may result harmfully or even fatally. If the damage is great enough to require surgery or suturing, by all means the veterinarian should be called. If it is not, the herdsman can dress the wound, keep it clean, and bring about healing.

If an animal loses its appetite and becomes nervous and feverish, it may be due to a more or less trivial digestive upset or to constipation, which a dose of salts or castor oil together with more careful feeding for a few days would correct. It might, on the other hand, be the beginning of an acute case of colic or the onset of some fatal disease, the symptoms of which are totally unknown to the herdsman, and in these latter cases it would have been much better to secure the services of the veterinarian as soon as the trouble was discovered.

Sometimes the male gets to be a bit slow and uncertain in service, or the females do not readily conceive. The herdsman may change the ration, start to feed minerals or vitamins, or try this or that panacea suggested by well-intentioned neighbors or friends. Perhaps the herdsman himself has had a bit of experience and training in massaging ovaries, breaking out cysts, and so on. Many herdsmen with training and experience can do these things and do them well. For many others no amount of available training or experience seems to suffice. They just don't have the knack. If you are in the first-mentioned class, you are fortunate, and you probably also have the good sense to be on your guard at all times and to call upon your veterinarian when things look as though they are beyond your own power to deal with successfully. If you are one who lacks the training, experience, or knack in handling such things, you will be well-advised to call on your veterinarian as soon as you notice something abnormal. And you will be still better advised not to let neighbors or others probably no better fitted than yourself start prescribing for or "treating" your animals.

Likewise, the time of parturition is a critical one for both mother and offspring, and again many herdsmen are capable of straightening up a fetus and of helping the dam to make a safe delivery. Other herdsmen are more or less helpless at this time if things are not normal. The same parallel might be pointed out regarding difficulties and abnormalities following parturition.

The veterinarian is all too often put in a bad hole to start with by being called only after a case has gotten really serious or by having not only the original trouble to contend with but also having to straighten out as best he can the bungling attempts of some not-too-intelligent animal nurse or midwife. From a purely selfish financial standpoint, overlong delay in securing the help of the veterinarian is generally "penny-wise and pound-foolish." The first prerequisite for success in animal breeding is the general and the reproductive health of our animals.

The need for veterinary services is a variable thing on all farms, and it need arises earlier under this owner or manager than it does under tha one. Probably every herd needs veterinary attention at times, and it i for each man to determine his own "when." The extent to which th owner or herdsman can take care of the simpler health cases of his animal also varies within rather wide limits, and each man must learn his ow abilities and more especially his own limitations. A good veterinaria in any case is an invaluable help to herd health, and, because this influences productivity and profits to such a large extent, the breeder, for hi own good, must study the problem and use veterinary service in such manner as will return the greatest profit to him. It certainly does no pay to be penurious in this field. It certainly does not pay to us "quacks" of any description. It certainly does not pay to remai ignorant of our own capabilities and limitations to render aid to ou animals, and, finally, and most important, it does not pay to dela overlong in getting needed medical care for abnormal, sick, or injure animals. A good veterinarian is about the best and most valuable frien a good breeding establishment can have. He merits fairer treatmen than has often been his lot in the past.

If a man is serving as herdsman or manager of a livestock-breeding farm, he will do well to arrive at a very definite understanding with the owner as to the procedure to be followed regarding the use of veterinary service. Are you as herdsman or manager expected to supply veterinary as well as animal-husbandry services? Few men are thoroughly trained in both fields, and the lack of training is almost sure to show up sooner or later and usually with some cost to the owner. Are you to provide what medical service you feel you are fitted to, and are you free to call on whatever veterinarian you wish to whenever you think you need his services? Are you to provide animal-husbandry services only and to notify the owner whenever you think veterinary services are called for? Is a veterinarian to be employed to make regular health examinations

TABLE 12.—REPRODUCTIVE PHENOMENA

	Age at puberty	Normal breeding season	Age first bred	Length of heat period	Length of gestation period	Rebred after parturition
Horses......	10–14 months	April–July	3 years	2–11 days	336 days	7–10 days or at next heat
Cattle......	4–8 months	Any time	15–30 months	1 day	281 days	60–90 days
Sheep......	4–8 months	September–December	18 months	2 days	147–152 days	Next fall
Swine......	3–6 months	December and June	9 months	3 days	114 days	3–5 days after weaning pigs

TABLE 13.—GESTATION TABLE

Date bred	Mare, 336 days	Cow, 281 days	Sow, 114 days	Ewe, 147 days
Jan. 1	Dec. 3	Oct. 9	Apr. 25	May 28
Jan. 6	Dec. 8	Oct. 14	Apr. 30	June 2
Jan. 11	Dec. 13	Oct. 19	May 5	June 7
Jan. 16	Dec. 18	Oct. 24	May 10	June 12
Jan. 21	Dec. 23	Oct. 29	May 15	June 17
Jan. 26	Dec. 28	Nov. 3	May 20	June 22
Jan. 31	Jan. 2	Nov. 8	May 25	June 27
Feb. 5	Jan. 7	Nov. 13	May 30	July 2
Feb. 10	Jan. 12	Nov. 18	June 4	July 7
Feb. 15	Jan. 17	Nov. 23	June 9	July 12
Feb. 20	Jan. 22	Nov. 28	June 14	July 17
Feb. 25	Jan. 27	Dec. 3	June 19	July 22
Mar. 2	Feb. 1	Dec. 8	June 24	July 27
Mar. 7	Feb. 6	Dec. 13	June 29	Aug. 1
Mar. 12	Feb. 11	Dec. 18	July 4	Aug. 6
Mar. 17	Feb. 16	Dec. 23	July 9	Aug. 11
Mar. 22	Feb. 21	Dec. 28	July 14	Aug. 16
Mar. 27	Feb. 26	Jan. 2	July 19	Aug. 21
Apr. 1	Mar. 3	Jan. 7	July 24	Aug. 26
Apr. 6	Mar. 8	Jan. 12	July 29	Aug. 31
Apr. 11	Mar. 13	Jan. 17	Aug. 3	Sept. 5
Apr. 16	Mar. 18	Jan. 22	Aug. 8	Sept. 10
Apr. 21	Mar. 23	Jan. 27	Aug. 13	Sept. 15
Apr. 26	Mar. 28	Feb. 1	Aug. 18	Sept. 20
May 1	Apr. 2	Feb. 6	Aug. 23	Sept. 25
May 6	Apr. 7	Feb. 11	Aug. 28	Sept. 30
May 11	Apr. 12	Feb. 16	Sept. 2	Oct. 5
May 16	Apr. 17	Feb. 21	Sept. 7	Oct. 10
May 21	Apr. 22	Feb. 26	Sept. 12	Oct. 15
May 26	Apr. 27	Mar. 3	Sept. 17	Oct. 20
May 31	May 2	Mar. 8	Sept. 22	Oct. 25
June 5	May 7	Mar. 13	Sept. 27	Oct. 30
June 10	May 12	Mar. 18	Oct. 2	Nov. 4
June 15	May 17	Mar. 23	Oct. 7	Nov. 9
June 20	May 22	Mar. 28	Oct. 12	Nov. 14
June 25	May 27	Apr. 2	Oct. 17	Nov. 19
June 30	June 1	Apr. 7	Oct. 22	Nov. 24
July 5	June 6	Apr. 12	Oct. 27	Nov. 29
July 10	June 11	Apr. 17	Nov. 1	Dec. 4
July 15	June 16	Apr. 22	Nov. 6	Dec. 9
July 20	June 21	Apr. 27	Nov. 11	Dec. 14
July 25	June 26	May 2	Nov. 16	Dec. 19
July 30	July 1	May 7	Nov. 21	Dec. 24
Aug. 4	July 6	May 12	Nov. 26	Dec. 29
Aug. 9	July 11	May 17	Nov. 31	Jan. 3
Aug. 14	July 16	May 22	Dec. 6	Jan. 8
Aug. 19	July 21	May 27	Dec. 11	Jan. 13
Aug. 24	July 26	June 1	Dec. 16	Jan. 18
Aug. 29	July 31	June 6	Dec. 21	Jan. 23
Sept. 3	Aug. 5	June 11	Dec. 26	Jan. 28
Sept. 8	Aug. 10	June 16	Dec. 31	Feb. 2
Sept. 13	Aug. 15	June 21	Jan. 5	Feb. 7
Sept. 18	Aug. 20	June 26	Jan. 10	Feb. 12
Sept. 23	Aug. 25	July 1	Jan. 15	Feb. 17
Sept. 28	Aug. 30	July 6	Jan. 20	Feb. 22
Oct. 3	Sept. 4	July 11	Jan. 25	Feb. 27
Oct. 8	Sept. 9	July 16	Jan. 30	Mar. 4
Oct. 13	Sept. 14	July 21	Feb. 4	Mar. 9
Oct. 18	Sept. 19	July 26	Feb. 9	Mar. 14
Oct. 23	Sept. 24	July 31	Feb. 14	Mar. 19
Oct. 28	Sept. 29	Aug. 5	Feb. 19	Mar. 24
Nov. 2	Oct. 4	Aug. 10	Feb. 24	Mar. 29
Nov. 7	Oct. 9	Aug. 15	Mar. 1	Apr. 3
Nov. 12	Oct. 14	Aug. 20	Mar. 6	Apr. 8
Nov. 17	Oct. 19	Aug. 25	Mar. 11	Apr. 13
Nov. 22	Oct. 24	Aug. 30	Mar. 16	Apr. 18
Nov. 27	Oct. 29	Sept. 4	Mar. 21	Apr. 23
Dec. 2	Nov. 3	Sept. 9	Mar. 26	Apr. 28
Dec. 7	Nov. 8	Sept. 14	Mar. 31	May 3
Dec. 12	Nov. 13	Sept. 19	Apr. 5	May 8
Dec. 17	Nov. 18	Sept. 24	Apr. 10	May 13
Dec. 22	Nov. 23	Sept. 29	Apr. 15	May 18
Dec. 27	Nov. 28	Oct. 4	Apr. 20	May 23

and to be entirely responsible for both the general and genital health of the herd or flock?

All of these systems may work under certain circumstances, but there will be much less loss and misunderstanding if a general policy can be adopted and followed. If you are the owner of the animals, the decision as to health policy is yours and should be made, and, when made, adhered to.

Summary.—For the production of strong, healthy offspring, it is first necessary that healthy individuals be selected to act as parents. In order to be sure of this first prerequisite, breeders will often have to enlist the aid of a competent veterinarian, who, by a thorough examination of the genital organs of both parents, and also possibly by an inspection of the spermatozoa produced by the male for their number, activity, normal structure, etc., will be able to render a clean bill of health or not, as the case may be, for the animals in question. The pregnant female should be maintained in a healthful, clean environment. She should receive suitable, properly balanced feeds, have a sufficient amount of sunshine and exercise, and not be required to do too much in the matter of production while engaged in her principal occupation, reproduction.

The breeding herd is a constant care, and the breeder must be quick to detect and combat the first signs of an attack by an invading germ. To do this successfully often requires periodic examination of all the animals in the herd by a skilled veterinarian. The only really successful way to combat trouble of any sort is to anticipate it.

Reproductive efficiency can be maintained through care in selecting healthy individuals and in feeding and managing them so that they may fulfill in a normal way the processes of reproduction. The offspring must be protected from infection from the moment of birth on through its entire life. In return for such feeding and care, there may be expected a normal, moderate amount of reproductive service from both males and females, in addition to the productive service that they may be rendering.

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CHAPTER IX

PARTURITION

The period of parturition is one of the most critical stages in the life of any animal. All the advantages gained in selecting genetically desirable and healthy parent stock and providing the very best of environmental and nutritional conditions through gestation can be dissipated at this time through carelessness or ignorance. Speaking generally, animals were more healthy and rugged in their wild state than since domestication. Then they ate natural feeds, lived close to nature, and brought forth their young in the fields and glens. All these conditions tended toward a minimum of sterility and of loss at parturition as far as the states of nutrition and sanitation were concerned. Domestication has altered this, and under artificial conditions animals cannot reach maximum efficiency without man's help and assistance. Death itself takes a large toll during parturition, and in many other cases the handicaps of joint ill, scours, etc., contracted at or immediately following parturition, detract to a marked degree from an animal's ultimate efficiency. The losses in most cases are due to ignorance of basic principles. The causes of parturition so far as now known have been discussed in an earlier chapter.

Cause of Parturition.—As indicated in Chap. VI, the mechanism of parturition resides largely in the endocrines, although the details of the hormonal reactions that lead to the expulsion of the young at term are not well understood. There is a certain rhythm to the whole of the reproductive process in each species. Parturition is fitted into this rhythmic scheme as indicated in Table 14.

TABLE 14.—ESTRUS—GESTATION RELATIONS

	Estrual cycle in days	Gestation, days	Ratio estrual cycle to gestation
Mare	21	336	1:16
Cow	20	280	1:14
Ewe	16–17	148–153	1: 9
Sow	19	114	1: 6

Parturition may be divided into several phases. The first phase consists of the dilation of the cervix and the loosening of the pelvic region. The second phase consists of the gradually accelerating con-

tractions of the uterine and abdominal muscles causing the actual expulsion of the fetus. The third stage is a continuation of the second, the muscular contractions beginning to abate but resulting in the expulsion of the afterbirth. A convalescent phase covers several days during which the uterus, cervix, and pelvis gradually return to the normal non-pregnant state.

Place of Parturition.—Parturition, or the act of giving birth to young, is a matter of vital concern in the attempt to produce healthy, vigorous livestock. If conditions are normal and the season permits, by far the best place for mares or cows to drop their young is in a pasture, because the instinct of the mother in these classes of livestock is generally superior to man's judgment and on pasture the animal is free to move about, is not rendered nervous through human presence, and the danger to the young from infection is practically nil. The obvious disadvantage in this practice is that conditions calling for assistance may of necessity be learned too late.

During this time ewes should be kept under fairly close surveillance in a lambing pen, and sows should be shut up by themselves in a house or pen. With proper thought and care the advantages gained, in all classes of livestock, from giving birth in the open can be duplicated in the maternity stall or pen with the distinct added advantage that assistance can be given if it is required. Maternity stalls or pens should be planned so as to give the highest degree of safety to the dam and her offspring and the greatest degree of convenience to the caretaker. The stall or pen should be roomy and there should be no protruding constructions that might lead to injuries. Mares sometimes lie down at parturition with their buttocks against a wall and some breeders obviate this possibility by building false walls that can be quickly moved. Doors into maternity stalls should be as wide as possible, in order to prevent injury to pregnant females. Maternity barns or pens should be well-ventilated, easily cleanable, and located where the animals contained can see and hear other animals with which they have been kept. Under no circumstances should parturition take place in a stanchion.

The sow's farrowing pen requires a guard rail placed about 8 in. from the wall and 8 in. from the floor. Sows kept in cement-floored houses should have a plank platform in one corner on which the sow can sleep. Many swine breeders are now using heated brooders in one corner of the pen, the heat of which early attracts the little pigs, and in this way chilling, stunted growth, and diarrhea are lessened.

Sanitation.—All maternity stalls or pens should be built or arranged so that maximum advantage can be taken of the most efficient germicide and also the most efficient growth promoter known, *viz.*, sunshine. Before putting any female into a maternity stall or pen, both the animal

and the pen should be thoroughly washed with a disinfectant solution. The coal-tar disinfectants, such as cresol, are good for this purpose, a 2 per cent solution to be used on the animal and a 5 per cent solution on the stall. The young are quite likely to suck or lick various parts of the mother's body; therefore, her whole body, more particularly the teats, should be kept clean. The floor and walls should be scrubbed thoroughly, care being taken to work the disinfectant well into the cracks and corners. Fresh, clean bedding should be used, preferably straw or hay rather than sawdust or shavings, as either of the latter is quite likely to get into the stomach or lungs of the newborn and cause inflammation. For sows, the hay or straw must be short enough so that the pigs cannot burrow under it, thus becoming hidden from view and running the risk of being trampled to death.

Time of Parturition.—A very necessary condition for successful parturition is that the breeder know when to expect it, and this predicates the keeping of a record of the breeding of all females. The record book, coupled with a knowledge of the normal gestation period and a sharp lookout for the unexpected, will enable the breeder to have things in readiness for the reception of the newborn. In some instances a knowledge of breeding dates and of gestation period is not enough to ensure that everything shall be in readiness, but without this information the case is well-nigh hopeless.

If a stall or pen is to be used, the females should be watched with even more diligent care than usual as the time for parturition approaches. They should not at this time be subjected to sudden changes of any kind in feed, exercise, or care. Moderate exercise is necessary to keep the muscles in good tone and to prepare them for the strain that lies ahead. The feed should be of a somewhat laxative nature—this point cannot be overstressed. The droppings must be watched closely, and, if, even in spite of proper selection of feeds, constipation develops, it must, for the safety and well-being of both mother and offspring, be quickly remedied. Feeds indicated at this time are pasturage, silage, roots, legume hays, bran, linseed-oil meal, and ground oats. In case of emergency, linseed oil or epsom salts may be administered. An abundance of good drinking water is also essential.

When bred, animals should be in fairly thin condition, but they should be gaining and should continue to gain slowly all through the gestation period, coming to the time of parturition in good condition regarding both quality and amount of flesh. Extremes in thinness as well as fatness should be sedulously avoided.

The females should be separated from the herd at least 1 to 3 weeks before parturition, so that danger of violent contact may be avoided. This will also enable the breeder to watch them more closely and will

provide opportunity for the animal to become accustomed to the stall or pen where parturition is to occur. Animals are naturally more or less nervous at this time and it is necessary that everything possible be done to allay their fears, which conduces to ease of parturition as well as to the safety of the newborn.

Preliminaries to Parturition.—Animals generally evidence a loosening of the ligaments and muscles in the pelvic region just previous to parturition, this being more noticeable in mares and cows. The pelvic region relaxes, the tail rises, the flanks and croup become hollow, and the enlarged abdomen drops. At this time, animals spring in their middles and start to make bag, with the udder becoming hard and tender, especially in primiparae. If the congestion in the udder becomes too great it should be relieved by milking before parturition. Most animals give evidence of approaching parturition by their general nervousness and fickle appetites. The mare whisks her tail, the cow bellows, the ewe bleats, and the sow grunts plaintively. Movements of the fetuses are often observable through the body wall or recognizable to touch. If not restrained, the female at this time will seek seclusion from its fellows, and the sow often starts to pick up straw, sticks, etc., with which to build a nest. Individuals, of course, vary in these manifestations, sometimes beginning to react a considerable time before parturition is due. However, these patterns of behavior and the breeder's record book of dates of matings taken together do give ample and accurate warning.

Act of Parturition.—If everything is normal and the animal has been properly fed and cared for, the act of parturition can usually be accomplished without assistance. Under these conditions the best procedure for the manager or herdsman, after checking up and seeing that all details have been properly carried out, is to go on with his work and let nature take its course. Here again the happy medium between too much attention and too little should be the aim. Meddling is often dangerous alike to parent, offspring, and owner. On the other hand, the day of parturition is rather a poor one to choose for a holiday. Mere human presence at this time is often objected to by the animal, especially by mares, which are particularly sensitive to human presence and will delay foaling as long as possible if such persists. Other animals, though not so sensitive, also prefer seclusion at this time. An occasional visit to note progress of events is always desirable and often profitable, and at this time an invaluable asset is the animal's confidence in her caretaker.

Labor pains set in from 1 to a few hours before final expulsion of the fetus. They are mild at first, lasting from a few seconds to 1 or 2 minutes with intervals of 15 minutes between. Their tempo, duration, and strength are gradually accelerated. The animal becomes increas-

ingly restless and nervous, shows evident signs of pain, and the skin becomes hot and dry. The pains are caused by rhythmic contractions of the longitudinal muscles in the wall of the uterus, which in this way begin the dilation of the cervix to allow passage of the fetus.

Even in the virgin the uterine muscles undergo very slight rhythmic contractions, as may be seen when the organ is withdrawn from the body and kept in salt solution at body temperature, and these contractions may be greatly increased by applying mechanical stimuli.[1]

At other than the heat period, these contractions are very slight, only increasing to great intensity at time of parturition, when the muscles of the uterus are very greatly developed. The dilation of the os is soon

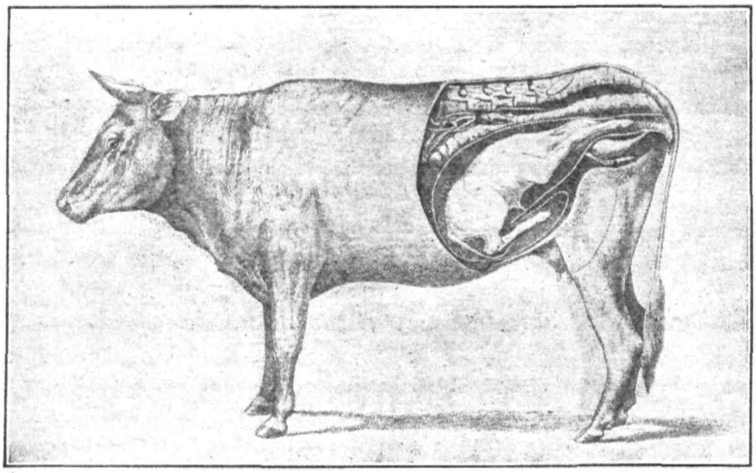

FIG. 59.—Normal position of calf in utero. (*From U.S. Department of Agriculture, Diseases of Cattle.*)

followed by the contraction of all the uterine muscles, as well as the abdominal muscles and the diaphragm, the contractions being followed by a short period of calm for rest. The combined contractions of the uterine and abdominal muscles soon force out the fetal membranes, which act as an elastic wedge to open the passages gradually. After protrusion, the water bag soon breaks, releasing part of the fluid; and the young, which in the meantime has turned first onto its side and then all the way over onto its stomach, soon makes its appearance.

The duration of parturition varies in different species of animals, being in the mare normally from 5 to 30 minutes; in the cow, 1 to 2 hours; in the ewe, 15 to 30 minutes for each lamb born; and in the sow, 10 to 30

[1] MARSHALL, F. H. A., "Physiology of Farm Animals," p. 188, Cambridge University Press, London, 1920.

minutes for each pig, with sometimes an interval up to an hour between the pigs.

The last stage of parturition consists of the expulsion of the fetal membranes, or afterbirth, and the man in charge should keep a careful watch to see whether or not this occurs normally. This may follow soon after birth, but, if it is delayed more than 24 hours, or 48 at the outside, steps should be taken to ascertain and obviate the difficulty. In case of retained afterbirth, the treatment most usually recommended at the present time is the insertion of iodoform tablets into the uterus, in order to prevent somewhat the danger from putrefaction, and also the daily douching with a normal salt solution. The manual separation of these membranes from the cotyledons is sometimes advisable. When expelled, the afterbirth should be removed at once and buried or burned. If this is not done, many sows, cows, and even some mares will eat this material. If, as sometimes happens, the young are born in the intact membranes, they should be liberated immediately in order to prevent asphyxiation.

The mare, cow, and ewe give birth either standing or lying, the sow reclining.

Types of Presentation.—The two normal presentations of a fetus are front feet first with the head resting between or on the knees, or hind feet first, the first-named being the most usual and showing the least complications. The pelvic passage is generally large enough to permit fairly easy passage of the forefeet and head. It is none too large, however, for the largest portion of the fetus, *viz.*, the thorax and shoulders. After the head has passed the vulva, there is often a short pause before the much greater effort now required. The dorsal vertebral spines over the shoulders are compressed backward, the thoracic cavity contracted and elongated, which diminishes its vertical diameter and permits passage through the pelvis. The posterior portion of the fetus generally passes through the pelvis without difficulty.

The normal hind-feet presentation, with the fetus lying on its belly and its back uppermost, is not quite so favorable as the anterior presentation. Birth usually takes longer with this presentation and the pinching of the umbilical cord may result in asphyxiation.

There may be various types of malpresentations, such as a buttocks presentation, back presentation, all four feet presented, and many others, some of which are shown in Fig. 60. Any malpresentation requires early recognition, together with a lot of skill and patience on the part of an experienced person, in order to prevent the death of the fetus and/or its dam.

Assistance at Parturition.—If, after reasonable time and effort have been expended, a female appears to be making no progress in parturition,

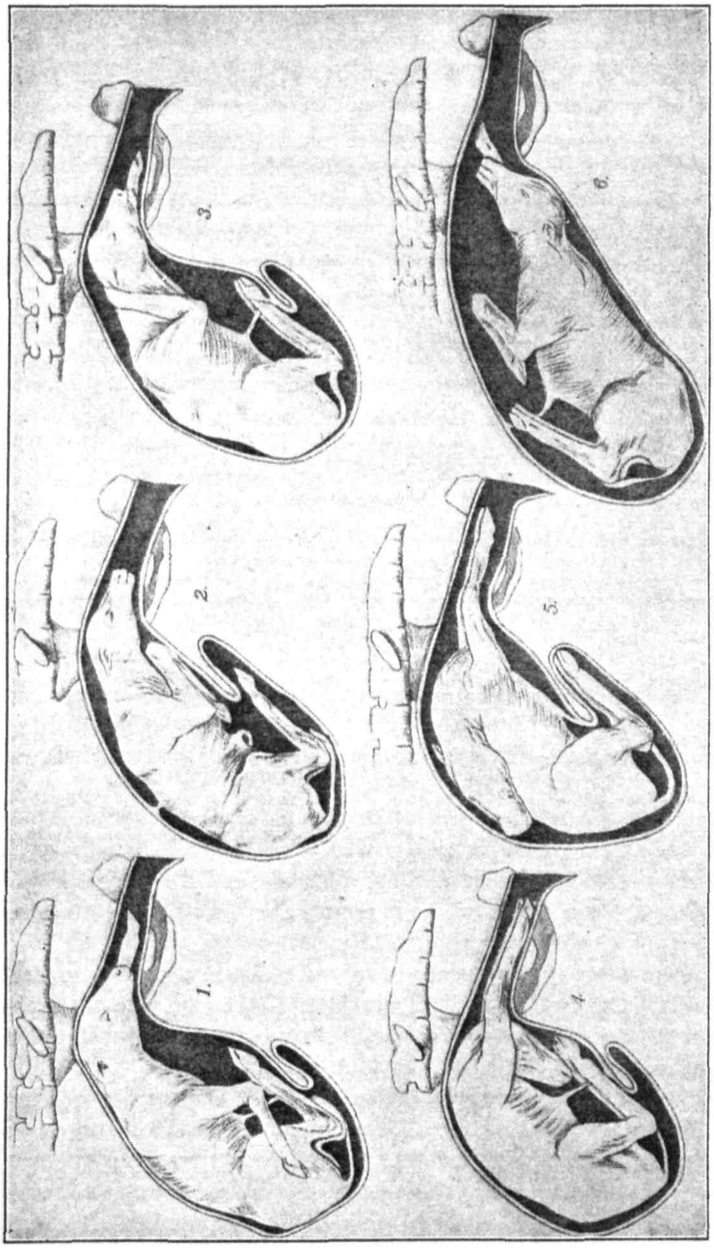

FIG. 60.—Abnormal positions of calf in utero. These must be corrected before parturition can take place. (*From U.S. Department of Agriculture, Diseases of Cattle.*)

it is advisable that an examination be made so that proper assistance can be rendered before the animal has completely exhausted her strength in futile efforts at expulsion. For such an examination the external parts of the vulva should be well-cleaned, the hand and arm should be thoroughly cleansed and lubricated, and the finger nails cut short. After proper precaution has been taken against injury, the hand, fingers held in a cone shape, is inserted into the vagina. There may be various types of malpresentations, such as only one front leg with the other turned back, one hind leg and the other stretched forward, abdominal or sacral presentation, head turned back on the side, head protruding with forelegs retained, all four feet presented, etc.

The cardinal features in the work of correcting the position of a fetus are cleanliness, quietness, gentleness, and perseverance, backed up, of course, by knowledge, skill, and experience. It is seldom necessary to resort to the knife at this time. If the presentation is normal, strength for expulsion merely being lacking, the feet can be grasped and a pull exerted downward and backward in conformity with the shape of the pelvis and the position of the young. The pull should only be exerted at the time the dam is in labor, never in the rest periods, except to maintain the gain that has been made. In correcting an abnormal presentation, it is often necessary to push the young well forward into the uterus and this should be done gently and during the rest period, not during the labor period. A small clean rope can be used to slip around the feet of a colt or calf, and a piece of No. 9 wire with one end bent into a hook to catch under the lower jaw is often useful as a last resort with lambs or pigs.

Pituitrin (pitocin), quinine, and other drugs are often used to stimulate uterine contractions in difficult labor, and oils have been found useful and often necessary in cases where the "water bag" breaks prematurely.

When parturition is unduly delayed or retarded, the fetus often dies. This may be due to twists or knots in the umbilical cord or to too long a stay in the passage, leading either to the stoppage of fetal circulation, or the depriving of the fetus of a supply of oxygen, or both. The same result is likely to follow premature breaking of the "water bag" with the consequent uterine pressure on the fetus or the too early disunion of the fetal membranes and the uterus of the mother. When labor has once started, it should be expedited in every manner that is not inimical to the safety of the fetus. The experienced caretaker can often cheat death through his own efforts, but there is no other time at which a skilled veterinarian can be of greater value to the progressive breeder.

Care of the Young at Parturition.—If birth is normal and the young are normal and vigorous, interference is not advisable. A colt or calf should be on its feet and sucking within an hour after birth, but, if not,

some assistance may be given so that the young animal can begin to get nourishment. The same applies also to lambs, where, in case of twins, the shepherd generally removes the first lamb until parturition is complete, when both lambs are allowed to nurse. In the case of sows, it is advisable for the herdsman to be present at parturition in order to remove the pigs when born, dry them, and put them in a safe place until parturition is complete, when all are allowed to nurse.

Losses from various forms of sterility are severe enough without adding to them by negligence at time of parturition. Sometimes it is necessary to remove the young from the membranes so that they can start breathing; whereas, on other occasions, it is necessary for the same reason to remove mucus from the mouth and nostrils. Many animals apparently stillborn can be induced to start breathing by slapping the sides, working the front legs and chest, as in restoring a man who has been submerged in water, blowing into the nostrils, tickling nostrils with a feather, etc. If an animal is stillborn, vigorous action on the part of the attendant will often cheat death, as will protection from the elements for those which have safely arrived.

With colts and calves, it is essential, soon after birth and in order to prevent joint ill or scours, to dip the stump of the umbilical cord into a solution of iodine kept in a wide-necked bottle. As previously mentioned, the dam should be cleaned thoroughly before parturition and no discharges from the vulva be allowed to soil the teats, to be later swallowed by the young in nursing. Little pigs' teeth, be they black or any other color, should never be pulled out—in fact, they should never be touched unless the sow gives evidence that the pigs are hurting her when nursing, in which contingency the sharp points of the teeth can be clipped off with a pair of small nippers.

Care of Mother at Parturition.—After safely delivering her young, the things a female needs most are rest and quiet, together with a moderate amount of temperate water. She should not be fed for 12 to 24 hours after parturition and should be started on feed very gradually. Gruels of bran and ground oats with perhaps a little linseed-oil meal are good at this time, together with a small amount of good-quality leguminous hay and some pasturage. The feed must be moderate in amount for two reasons: (1) a return to the normal condition of the dam's system will be hindered by overfeeding, and (2) the presence of too much milk in the udder as a result of overfeeding is sure to cause scouring in the young, which is always a serious drawback to normal health and growth. The wise herdsman never feeds a nursing female until he has observed the character of the droppings of the young, and at the first sign of scouring the dam's feed should be reduced. Feed given to an animal suffering with a bacterial infection, such as scours, will not be properly digested and assimilated.

Some calves may have already become infected in utero and may scour immediately after birth. All feed should be withheld from such animals for periods up to 72 hours, and calf scour serum should be administered.

Cows should not be milked out completely immediately after calving, as this is likely to bring on milk fever. It is necessary, however, to see that some milk is drawn from all the quarters, because, if any of the quarters are left full of milk for too long a time, they may be injured.

From 2 to 4 weeks should be allowed to get the female back to full feed. Mares can go back to light work in 2 weeks. Care must be exercised that the foal left in the stall cannot harm itself, because it will be quite restless without its dam. The foal should be allowed to nurse midmorning and midafternoon after the mare has been allowed to cool off, if warm, and after her udder has been washed.

If parturition has been difficult or even where it has been normal there is danger of the mother's genital tract having been injured or invaded by harmful bacteria. With valuable breeding animals, it would no doubt always be a wise and, in the long run, profitable procedure to purchase some service and attention from a veterinarian in order that females return to a normal healthy post partum condition as surely and as quickly as possible in order that their future breeding worth may be conserved.

Feeding and Care of Offspring.—There are four stages in feeding and nourishment of any animal. In the first stage, immediately following fertilization, the zygote lives upon the energy supply provided in the egg itself, the yolk. In the second stage, the developing embryo lives upon "uterine milk" and on materials carried to it in the mother's blood stream. The third stage is that from birth to weaning and is the one we are primarily concerned with in this section. The fourth stage is, of course, the one following weaning when each animal must take care of its own nutritional needs.

The breeder can do a lot to ensure strong healthy offspring by properly feeding the pregnant female. He can continue this insurance following parturition by so feeding the mother that sufficient milk will be produced for the young. For a time following parturition most young animals live entirely on milk. The milk secreted by the dam for the first few days following parturition is called *colostrum.* This differs from later milk in many ways, especially in being more concentrated. Colostrum is very high in its protein content, especially the globulins. It is rich in vitamin A and perhaps other vitamins and contains many antibodies against bacteria and other foreign substances that have been developed in the mother and are passed on to the offspring in colostrum in order to fortify the young against the invasion of harmful organisms, which provides a passive immunity until an active one can be built up. Colostrum also stimulates the alimentary tract to begin to pass out waste products, the

first passed being known as *meconium*. Livestock breeders know from experience that the young have a better chance of survival if they get colostrum from their dams. If this for any reason becomes impossible, properly modified cow's milk, to provide the proper species balance between protein, lactose, and fat and to include sufficient vitamin A, castor oil to effect bowel movement, and blood serum to provide antibodies, can and should be substituted.

It has long been recognized that in general the young of one species thrive better on milk of their own kind than on that of another species. Furthermore, the sooner after birth the milk of another species is substituted for milk of the same species, the more unfavorable is the outlook for the young animal. The results of some studies published by Bilek are cited as indicating that some of the unfavorable effects so often obtained from feeding milk of another species may well be attributed to qualitative rather than quantitative differences. In these experiments, cow's milk and goat's milk were fed to the young of several species. The different species did not react alike. Kids used both milks equally well, while calves reacted to goat's milk with severe gastrointestinal disturbances which lasted as long as goat's milk feeding continued. Pigs showed no disturbance on cow's milk but reacted to goat's milk in a fashion similar to that observed in the calves. Foals showed a stubborn diarrhea when fed undiluted cow's milk but not the slightest disturbance on goat's milk. Since the two milks are very similar in percentage composition, the results indicate the presence in the milk of substances incompatible or toxic to the animals that reacted unfavorably. It is suggested that the incompatible factors are proteins.

It is known that the presence of a foreign protein undigested in the circulating blood is more or less toxic to an animal and may produce a sensitization to further additions of the foreign protein. It has been established that the newborn animal normally absorbs considerable protein undigested through the gastrointestinal wall. Although this apparent permeability decreased rapidly after birth, it probably does not cease abruptly, since as Ratner has shown, it still occurs to some slight extent in about 50 percent of adults. The possibility of the absorption in the very young suckling of appreciable amounts of undigested and sensitizing foreign protein might be a major factor in the incompatibility of the milk of one species for the young of another.[1]

The young of all species will be better off if they are allowed to suckle for at least 3 or 4 days. After this, they can be hand-fed if desired, although this is seldom practiced except with dairy calves. Many systems of feeding dairy calves have been devised and are available in various books and bulletins.

Colts, calves, lambs, kids, and pigs will begin to nibble at the dam's feed in from 2 to 4 weeks after birth. They should then be supplied with suitable fine roughage and with suitable grain mixtures, preferably in a creep to which the dam does not have access. For colts, a mixture of 2

[1] EARLE, I. P., Food and Life, p. 508, *U.S. Dept. Agr. Yearbook*, 1939.

parts cracked corn, 4 parts crushed oats, 2 parts bran, and 1 part linseed-oil meal by weight has been found to give good results. For calves, many starters and meals have been developed and are available under trade names. They can also be home-mixed from such ingredients as corn meal, ground oats, bran, middlings, and linseed-oil meal. Similar starters or home-mixed rations will also serve for lambs and kids. Pigs may also be fed home-mixed rations of corn, middlings, and protein supplements such as fish meal or tankage. Pigs should also be supplied a mineral mixture such as bone meal 38 parts, calcium carbonate 39, sodium chloride 20, ferrous sulphate 2.5, copper sulphate 0.25, and potassium iodide 0.03 parts by weight. In order to prevent anemia in pigs, many breeders paint the sow's udder daily with a solution of iron and copper or place fresh clean sod or dirt where the little pigs can get it.

For maximum growth and well-being the young must be comfortably housed in sanitary, safe quarters and must be properly fed both by their mothers and through their own efforts. To keep young animals on feed and gaining steadily from the day of birth is an art, gained only through experience. For maximum eventual returns, proper care and nutrition are indispensable. Any young animals do best if fed regularly, often, and moderately. They should clean up their feed with a relish and look for more, the secret of success being to keep them a little hungry. Misguided kindness in the form of too much feed must be avoided.

If the young are ever to achieve the maximum of their inherent capabilities, they must get started early along the proper path and must be kept moving. Normal healthy parents are the first prerequisite, clean maternity stalls the second, proper feeding and management of the lactating female the third. The young themselves will soon (one to three weeks) evidence a desire to eat something besides milk. This desire should be satisfied not with shavings and sawdust but with good pasturage, fine-quality hay, and a suitable grain mixture. Remember that whole milk, and more especially skim milk, is very high in protein. Along with a suitable quantity and quality of milk from the dam and such other feeds as just mentioned should go a sufficient amount of exercise, preferably at pasture and in the sunshine. If worms are prevalent, it will be necessary to remove all green growth from lamb and pig runs and to put the pigs and the lambs on fresh pasturage that has not had sheep or sows on it for at least 12 months. The greatest drawbacks to the successful rearing of desirable young are overfeeding and underexercising.

Constructive breeding implies that records are to be kept. With the young animal this starts at birth. Among other things, the record should show the animal's sire and dam, the length of gestation, the character of parturition (normal or otherwise), single or multiple births, weight of the offspring, their general condition, number born weak or dead, and any

other pertinent data which will be of service when the breeder is deciding whether or not to breed the dam again or whether or not to save her offspring for breeding purposes. Parturition is a busy time for the herdsman, so that if he does not get his records then and there, they are likely never to be secured.

If animals are to be marked in any way, it should be done early and before there is any chance for making mistakes. Pigs are usually marked by notching the ears; *e.g.*, a notch in the outer edge of right ear stands for 1, outer edge of left ear for 3, inner edge of right ear for 10, and inner edge of left ear for 30. Lambs and calves are best marked by metal tags or calves by tattooing. If the tattoo fades, it can be made permanent in the other ear at about two years of age.

Complications before Parturition.—During gestation, many complications can arise that will interfere with normal parturition at term. Superfetation or the successful breeding and conception by an animal already pregnant is one of this sort. When impregnated, most animals do not normally ripen an egg and again come in heat until they have delivered the embryo or fetus. Occasionally, however, they do, are bred, conceive, and carry offspring of different ages in the uterus. Cases have been reported in the mare, cow, ewe, and sow as well as other animals. Hering reports a cow giving birth to normal calves in August and the following December. Muller reports the case of a sow giving birth to a litter of 11 pigs 23 days after she had farrowed 6 normal pigs. In many cases, the younger embryos are expelled when the older ones reach term and the former do not live.

Extrauterine pregnancies have been known to occur in the ovary, tubes, abdomen, vagina, or between the serous and mucous coats of the uterine wall. Such cases usually result fatally, or, under favorable conditions, the fetus may become mummified and persist for years, the latter usually causing an absence of heat and sterility.

Fetal monsters (teratoma) in the form of unorganized fleshy masses, sometimes containing skin, hair, teeth, and sebaceous glands, uterine cysts, or the collection of large amounts of serous fluid in the uterus, are often mistaken for true pregnancies.

Colic in mares, constipation, depraved appetites, and edematous swellings of the lower limbs and along the underline are often found in pregnant animals. They are generally due to improper feed, lack of exercise, etc. Still another occasional abnormality in gestation is the overproduction of amniotic or allantoic fluids. This eventually greatly distends the abdomen and is usually fatal to the fetus. It occurs quite often in wide outcrosses such as those between the bison and ordinary cattle, which indicates a genetic basis in these cases. It is thought that it may also be caused by poor feeding, torsion of the umbilical cord with

consequent interference with fetal circulation, or through malfunctioning of the heart or liver of the fetus.

In addition to the above, pregnant animals sometimes suffer attacks of paralysis, cramps, hysteria, coughing spells, albuminuria, and toxemia, the causes for all of which are rather obscure. Good feed, suitable shelter, and exercise will tend to minimize their appearance or effects.

Accidents caused by slipping, crowding through narrow doors or gates, cruel treatment, or careless handling often result in death or expulsion of the fetus or both, as also does Bang's disease. Such things as prolapse of the vagina, hemorrhage or rupture of the uterus, or uterine hernia are not unknown among pregnant animals. Occasionally the fetus cannot be discharged at term, leading either to putrefaction and eventual absorption or to mummifaction, sterility often following in either case.

The 4- to 11-month gestation period in farm animals is fraught with many difficulties and dangers. Some of its abnormal manifestations seem to be beyond the immediate control of the breeder. There are, nevertheless, many things that he can do to help ensure a safe passage through gestation for his females, many more than he apparently sometimes realizes or is willing to pay attention to.

Complications at Parturition.—Parturition may be complicated by malpresentations, lack of strength to expel the fetus, extreme nervousness and excitability, and many other things that may imperil the life of either the mother or offspring or both. Proper feed, exercise, judicious handling of mares, and drying off of dairy cows together with the sort of treatment that will make the female welcome the presence and attention of her caretaker will do the most to cut down losses and deaths at this critical time.

Difficult labor is called *dystocia*. It may be due to some abnormal condition in the mother (maternal dystocia) or to some abnormal condition in the fetus (fetal dystocia). It occurs most frequently in animals kept under the most unnatural conditions, *viz.*, the dairy cow. In the dam, they are generally due to pelvic abnormalities, displacement or changed relations in the uterus, or morbid or diseased conditions of the genital tract. In the fetus, they are due to malpresentations or to various diseases, malformations, tumors, or other abnormalities either of the fetus itself or its surrounding fluids or membranes. The breeder generally needs help in order to correct any of these abnormal conditions, and we would again urge that not too much time be lost in getting it if conditions or behavior seem abnormal.

Complications Following Parturition.—The strain involved in parturition plus the avenues of infection that are automatically opened by it render the dam particularly susceptible to complications following parturition. They may take many forms, from retained placenta,

hemorrhage, eversion of the vagina, uterus, or bladder to lesions in various parts of the genital tract or the invasion of the tract by various organisms, causing inflammation of the uterus, cervix, or vagina, often accompanied by the formation of pus. In addition, milk fever, septicemia, paralysis, convulsions, and many other abnormal or diseased conditions may follow parturition. Surely the lot of the dam at this time is not an enviable one. The least the livestock breeder can do is to use all the precautionary measures regarding feed, care, and sanitation he can lay hold of and not begrudge or delay too long in getting the best skilled attention he can secure whenever it becomes necessary to have it.

Summary.—In this chapter we have discussed the causes and processes of normal parturition. Understanding something of the complicated process should make us, as livestock breeders, a bit more appreciative of the dam's situation during this critical time. With intelligent care and forethought, most of our animals can be brought through parturition unscathed and their offspring gotten off to a good start on the road to their eventual service in production or reproduction. We have seen that the process of parturition is often beset with a multitude of complications. If we are going to succeed in livestock breeding, we must learn to handle our animals intelligently at this time—the time and process on which the whole structure of animal breeding ultimately rests, for it has to do with the safe induction into the world of the animals that we hope our genetic planning and selection have given a good chance of being superior to their forebears.

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CHAPTER X

STERILITY

Sterility is present to a greater or less extent in all breeds and flocks and entails enormous financial loss annually. A clean, fertile herd or flock can be had and maintained, provided the proper thought and effort are expended. The task, however, is not an easy one and requires the most efficient technique for its successful achievement. Only about 60 per cent of mares bred drop living foals, and, although the percentage in cattle, swine, and sheep is no doubt somewhat higher, it falls far short of 100 per cent.

The losses from partial or complete sterility in dairy-cattle herds are probably greater than in most other classes of livestock. One of the reasons for this is, no doubt, the fact that dairy cattle are generally kept under the most unnatural conditions; *i.e.*, they are housed more closely, thus often able to get but little exercise, and are fed in such a way as to stimulate their productive capacity to the utmost. Speaking generally, conception is more difficult of attainment in this class of animals, and in addition they no doubt suffer more from genital derangements, abortion, etc., than most other classes of farm livestock. If the average breeder were to compute the breeding efficiency of his herd or flock by dividing the number of young born, or, better, raised to weaning age yearly, by the total number of females bred or of breeding age, he would in many instances receive a very rude shock. Not only is there a loss from the lack of young stock to sell, but, in cattle especially, the returns from milk production will also be seriously lessened while the temporary or permanently sterile animals must continue to be fed.

There are a great many things or combinations of things that may lead to partial or complete sterility, and a complete discussion of the topic is not here possible. The purpose of this chapter is to delineate the subject in its broad outlines and to impress upon the student and breeder the necessity for continually keeping the subject in mind. The first prerequisite for successful breeding is health, especially breeding or reproductive health, in all the animals making up the herd or flock. With this primary major item properly taken care of, marked success in breeding is possible of achievement; without it, success just is not possible.

Herd-health Associations.—A few herd-health associations have now been formed in the United States, some in connection with artificial-

breeding work. One of the first and most successful was formed in Middlesex County, Massachusetts, by the county agent, Herbert Brown. The general plan of operation is to hire a veterinarian to make regular visits to the farm to check on the general breeding health of the herd, to diagnose pregnancies, and advise generally on reproductive efficiency.

This plan has everything to recommend it. In operation, under a competent veterinarian and with reasonable cooperation from owners, everyone concerned stands to gain. The veterinarian has an assured income that is the due of any trained, hard-working individual. The breeder has a herd that breeds. He, therefore, also has an assured income. His veterinary fees are no greater, he has the money with which to pay them, and he is using veterinary medicine in the most intelligent manner possible, *viz.*, to prevent rather than to try to cure breeding or other derangements in his animals. This is socialized medicine for livestock. Perhaps we will eventually have the intelligence to apply the principle to ourselves and our families. What chaos there would be if no one attended school until he or she had grown up and gone out into the world, there to discover his or her ignorance. Early schooling is designed to fit us for active participation in the world's work. In like manner, herd-health associations are designed to fit our animals for their work in breeding and production.

There are many causative factors of sterility. We will discuss them under certain broad headings.

Genetic Causes of Sterility.—Certain forms of sterility apparently have a genetic basis. The work of Bridges with Drosophila has shown that a male of sex-chromosome constitution XO (due to nondisjunction) is sterile. Evidently the absence of a Y chromosome in this species renders an animal sterile.

An instance from practical breeding history which appears to belong to this category is that of barrenness in Bates' famous Duchess family of Shorthorns. This family was noted for superior individual excellence, consequently breeders, naturally desirous of maintaining this excellence, followed a practice of breeding within the family, an example of which is given in Fig. 61. But the family was

Duchess 55th	4th Duke of Northumberland (3649)	Short Tail (2621)	Belvedere (1706)
			Duchess 32nd
		Duchess 34th	Belvedere (1706)
			Duchess 29th
	Duchess 38th	Norfolk (2377)	2nd Hubback (1423)
			Nonpareil
		Duchess 33rd	Belvedere (1706)
			Duchess 19th

FIG. 61.—Pedigree of one of the latest Duchess cows, illustrating system of linebreeding followed in maintaining the family. Duchess 55th produced two calves.

tainted from the beginning with the curse of barrenness. . . . Shortsighted breeders at the time considered it a fortunate circumstance that Duchess cows were so often barren, for it kept down the number of individuals of this favorite strain and resulted in prices correspondingly high. But as a result of barrenness the strain eventually ran out completely. In Fig. 62 an attempt has been made

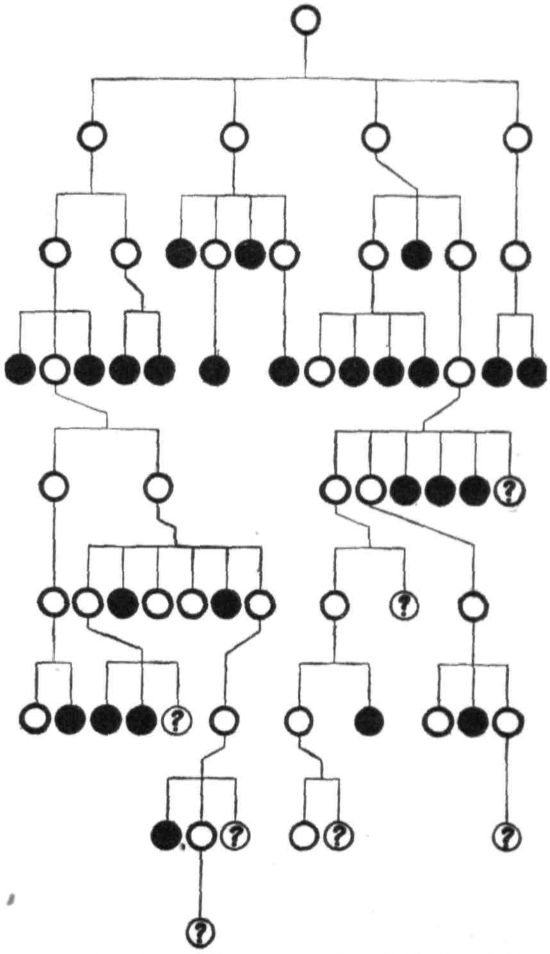

FIG. 62.—Illustrating inheritance of barrenness through the female line of the Duchess family of Shorthorns; barren cows represented by solid black circles. (*From Babcock and Clausen, Genetics in Relation to Agriculture.*)

to show diagrammatically how barrenness was inherited in this family. The diagram is not complete, for it includes only the females in the family. Nevertheless it brings out very forcibly how barrenness occurred very early in the family history, and how it reappeared in about the same proportion of the total population throughout its history. Far from showing an intensification of the

defect as a result of inbreeding, this diagram merely illustrates the heredity of a defective family trait.[1]

Probably most breeders of some years' experience can recall certain females in their herds of 10 or 20 years ago that now have no descendants in the herd. If a breeding chart of the herd has been kept or can be made, such lines are practically sure of being evident. Some of these lines perhaps disappeared because of poor type or poor production or both. Others, no doubt, have disappeared because of too low rates of reproduction or no reproduction at all. Whether this has been due to poor management or to poor genetic make-up is perhaps hard to determine, so to be conservative we will say that some of it has been due to one, some to the other, some to both.

Among breeds, especially those with multiple births, there are demonstrated variations in rates of reproduction. Among individuals in a breed or among grade animals similar differences are to be found, and some of these differences undoubtedly have a genetic basis. There may be no specific genes for fertility, but genes undoubtedly control the size, normality, and functional activity of the pituitary, ovaries, testes, and accessory organs of reproduction. It perhaps is somewhat of a contradiction in terms to speak of the *inheritance* of sterility. Nevertheless, rate of functional activity of the whole reproductive system undoubtedly has a genetic basis, and, of course, this, like all other bodily activities, is quite susceptible to environmental influences. Sterility perhaps cannot be inherited, but genes causing low rates of fertility or even the complete absence of fertility may be and at times are transmitted from either or both parents.

Lethal genes that lead to the death of the organism before the normal span of years for the species has been achieved might also be considered genes for sterility, for dead animals do not reproduce.

Systems of Breeding and Sterility.—The fact that too wide crosses, *e.g.*, bison and cattle, or horse and ass, often result in sterile or relatively infertile offspring, coupled with the fact that too close inbreeding often produces similar results as far as sterility is concerned, is further proof that some sterility is caused by genes.

In selecting breeding stock, therefore, one should be careful to make his selections only in strains or families that by their actual records of reproduction have proved themselves to be at least relatively free from genes which lower fertility. It is often observed that animals of a strain which have been closely inbred for a number of generations are sterile when mated among themselves but fertile with other nonrelated strains.

[1] BABCOCK, E. B., and CLAUSEN, R. E., "Genetics in Relation to Agriculture," pp. 555–556, McGraw-Hill Book Company, Inc., New York, 1918.

In fact, the above condition sometimes applies as well to animals that are not closely related. In a great many of the experiments on inbreeding, there have gradually developed a loss of vigor and a lowering of fertility. For instance, Weismann's and Von Guaita's work with mice gave the following results.

TABLE 15.—DECREASING FERTILITY IN INBRED MICE

Generation	Average per Litter
1–10	6.1
11–20	5.6
21–29	4.2
29 and 30	3.5
31 and 32	3.6
33 and 34	2.9

Similar work by Ritzema Bos on rats gave the following results:

TABLE 16.—DECREASED FERTILITY DUE TO INBREEDING

1887	1888	1889	1890	1891	1892
7 1/2	7 1/7	7 12/17	6 21/36	4 7/13	3 1/5

This effect of inbreeding is not universal, however, as King reports on two series of rats (A and B) inbred, litter brother and sister, for 25 generations:

> Data given for the A series of inbreds comprise 1,752 litters containing 13,116 individuals, or an average of 7.5 young per litter; records for the B series of inbreds include 1,656 litters, having a total of 12,336 members, or an average of 7.4 young per litter. The two series combined comprise a total of 3,408 litters, which contained 25,452 individuals. For the entire strain the average size of the litter was 7.5 young . . .
>
> A comparison of the data for the inbred strain with data for litter size obtained from a series of stock Albinos reared under the same environomental conditions as the inbred strain shows that each litter of the stock series was relatively smaller than the corresponding litter in the inbred group. For the entire series of 424 stock litters the average size was 6.7 young per litter. This average is 0.8 less than the average for litter size in the inbred strain.[1]

Crossbreeding, on the other hand, where the resulting individuals are not completely sterile, as is the mule, often produces plants or animals that are more vigorous in all respects than their pure parents and are often more fertile. This increased vigor is termed *heterosis* or *hybrid vigor*. The exact cause of these phenomena in inbreeding and in crossbreeding is not fully understood. It has been suggested, however, that the germ plasm of all species probably carries some inhibiting factors, which, if true, explains why inbreeding often does result in lowered fertility, because

[1] KING, H. D., "Studies in Inbreeding," 97 pp., The Wistar Institute, Philadelphia, 1919.

these inhibiting factors are intensified, and why crossbreeding often results in increased fertility, because each diverse parent supplies to the offspring factors that tend to dominate and offset the expression of the weak characters supplied by the other parent.

Among species hybrids, there is a wide range of ability to reproduce, *viz.*, from a point of increased fertility over the parents down to a point of absolute sterility. The mule and the hinny, the former a jack-mare cross and the latter a stallion-jennet cross, are both sterile, as are also the horse-zebra crosses. Babcock and Clausen report one reference to fertile male hybrids between the zebra and the ass. The researches of Wodsedalek on the reproductive cells of the mule show abnormal reduction divisions during spermatogenesis, which should logically result in imperfectly formed and functioning germ cells. If the hybrids in any cross have characteristically a different number of chromosomes, it is difficult to see how the reduction divisions could be normal and result in the production of functional germ cells. Even if the chromosome numbers were the same in the two species, physiological incompatibility might be present.

In many crosses between species of Bovidae, as common cattle with bison, gaur, gayal, and yak, the female is fertile and the male sterile. Among domesticated birds, as in the sterile hybrids between various species of pheasants, the sexual organs are imperfectly formed, and there is a strong suspicion that sterility may be due in part to imperfect sex determination resulting from hybridization. Even aside from this difficulty which is zygotic, there is the further one that the chromosome condition in these hybrids may be unbalanced and the differences in genetic content of the chromosomes may be so great as to prevent functioning of the gametes which are formed. The sterility of species hybrids is in quite a different category from that of the sterility occurring within species.[1]

Davenport observes in regard to hybrids that "it is safe to assume that about all the possible fertile hybrids were long ago produced in nature, and either went down under natural selection or became good species before they came into our hands."

Anatomical Deficiencies or Derangements.—There are a great many deformities and departures from the normal that may render an animal sterile. In the male are found anorchidism, or lack of testicles, and cryptorchidism, or the retention of the testicles in the abdominal cavity. The lack of active spermatogenesis renders these animals sterile. If one testicle is present in the scrotum, the animal is probably fertile, although it is a grave question as to whether or not any animal ought to be used for breeding purposes if it shows genital abnormalities of any sort, for they may possibly be inherited. Malformations of the penis or other parts of the male genital tract may render normal service and deposition of

[1] Babcock, E. B., and Clausen, R. E., "Genetics in Relation to Agriculture," p. 591, McGraw-Hill Book Company, Inc., New York, 1927.

spermatozoa in the female genital tract impossible. Because the anlagen for both sets of reproductive apparatus are present in the early embryo, it should occasion no surprise to learn that occasionally the mechanism does not function normally but instead produces various types of abnormalities. The gonads may contain both imperfect seminiferous tubules and Graafian follicles, or one may be a testis, the other an ovary, and in such cases normal functioning is generally impossible. Likewise, the two sets of primitive ducts, Wolffian and Müllerian, may each at times give rise to an incomplete or imperfect set of male or female accessories, or sometimes some of each, and again normal functioning is interfered with. The possibilities of abnormalities occur also with the external genitalia, penis, clitoris, scrotum, and vulva, and these are occasionally found.

In the female are found various deformities such as double or deformed cervix, double uterus, single horn of uterus, abnormally formed or distributed cotyledons, persistent hymen, strictures, etc., some of which a veterinarian can obviate, provided the worth of the animal justifies the expense. Also either umbilical or inguinial hernias may occur in either sex and interfere with normal breeding activities, and in some species this defect has been shown to be hereditary. In all cases of deformities, the matter of the possible transmission of the deformity or weakness should be considered carefully before deciding to retain the animal in the breeding herd or flock. The freemartin heifer which has had the misfortune to have its extraembryonic blood vessels fuse with those of the male twin, will evidence varying degrees of abnormality throughout its genital tract and will of course be sterile.

Hormonal Aberrations.—The normal functioning of the hormones having to do with various phases of reproduction has been discussed in a previous chapter. This whole mechanism is very delicately balanced, and much yet remains to be learned concerning the actions and interrelations of the whole of the endocrine system. Since it is so intricate and so delicately balanced, we should expect that it may often function at something less than maximum efficiency. Although the hormones have had some use as therapeutic agents in increasing degrees of fertility, such usage has not been widespread. That this field will become better known, more widespread in its use, and of great value to livestock breeders seems, like anything, but a rash guess. Since the anterior-pituitary, testicular, ovarian, corpus luteum, and placental hormones have now been purified and can be produced from biological or synthetic sources, it is to be expected that increased research will further delineate their functions and interrelations and that breeders will use this knowledge in a practical way to obviate partial or complete sterility.

Here again a word of caution seems justified that we do not, in the process of overcoming sterility by artificial means, overlook the fact that

these deranged hormonal activities may have a genetic basis. In the human being, we have learned how to circumvent the action of many bad genes, and in so doing we have perpetuated them. There would seem to be neither necessity for nor any advantage in repeating the process in animals.

Psychological Aberrations.—That animals differ from man in degree rather than in kind regarding psychological as well as physiological characteristics needs no argument. That psychological aversion to mating exists in animals as well as in man has had many demonstrations,

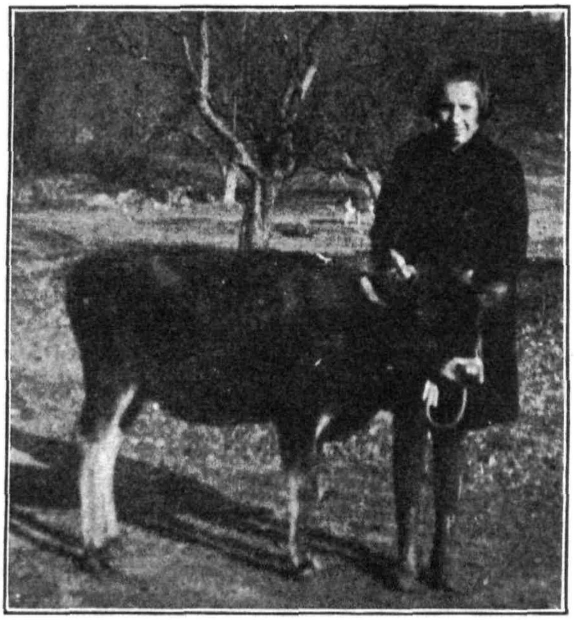

FIG. 63.—The sire and dam of this calf were twins.

although it would perhaps be difficult of demonstration as an important cause of sterility in the former.

Likewise, genetic incompatibilities are probably the cause of a small amount of sterility among farm animals. Their presence both in too wide and too close breeding has already been referred to. Their manifestations undoubtedly extend all the way from the inability of certain sperm to fertilize the egg on through the death of the embryo or fetus at varying ages. Hybrids are no doubt often sterile because of incompatabilities of the genes, although this condition may be obviated in tetraploids, where the double set of chromosomes permits normal pairing and cell division. Muller has succeeded in securing fertile females in a cross between two

races of Drosophila (*melanogaster* and *simulans*) that are always sterile by using triploid females and X-ray-treated males. In this way, certain of the male chromosomes were deleted, and, when such a sperm happened to fertilize an egg with the extra chromosome that had been lost from the sperm, cell division and growth became possible, because the incompatability between the genes had thereby been sufficiently reduced.

At times, females become so excitable at heat and breeding that the normal processes of retaining the semen and of fertilization are interfered with. Likewise, the male at times fails to have a complete ejaculation or deposits the semen just inside the vulva instead of at the anterior end of the vagina, thereby lowering the degree of fertility. Troubles of this nature may be overcome through artificial insemination.

Physiological Deficiences or Excesses.—As noted earlier, the spermatogenic and ovogenic tissues are laid down very early in the development of the embryo. If the egg and sperm that have united to produce the new individual have been normal and unimpaired, and if the uterine conditions and the mother's health and feed are normal, the development of the germ plasm of the embryo and fetus proceeds in a normal fashion. There are no viable germ cells in the offspring at birth. The primordial tissues, however, are present and developmental processes are active, although these do not eventuate in viable spermatozoa or ova until the age of puberty. Obviously many things might interfere with the process at any time.

If the young animal is not fed so as to grow at the normal rate for its species, the production of germ cells will be delayed. If the growing ration is unbalanced, of poor quality, or lacking in any essential element, or if the young growing animal does not get sufficient exercise and sunshine on good pasture, reproductive activity may not be normal. This may extend all the way from a condition of complete absence of mature spermatozoa or ova to one where the sex cells are produced in apparently normal numbers but of too low functional activity to eventuate in viable offspring. Spermatozoa and ova may be present but in such a weakened condition that fertilization and normal development are not possible.

At the other extreme, there are no doubt occasions when the young animal is fed too liberally, the excessive fat and generally attendant lack of exercise yielding weak or nonviable germ cells. Spermatozoa may be entirely lacking in the seminal fluid, owing to a variety of causes. In some animals, put into too high condition, spermatozoa are secreted in the testicle, but the excess fat packed around the tubules and tubes leading from the testicles entirely close them so that the spermatozoa cannot escape. Inflammation of the epididymi or vasa deferentia may cause their complete closure, so that spermatozoa, normally secreted, cannot escape at copulation. At times, too, a fibroid degeneration of the testicles

is found. This is caused by the overdevelopment of the interstitial tissue of the glands with compensating atrophy of the secreting tissue.

Although not established experimentally, it is probably true that conditions similar to those discussed in the previous section, tending to cause an absence of spermatozoa in the male, also prevail correspondingly in the female, tending to cause the absence of functional ova, though the animal may come in heat and mature ova in the ovary. Another phase of this problem in the female is evidenced by certain females in which the ova do not reach full development and in which ovulation does not occur.

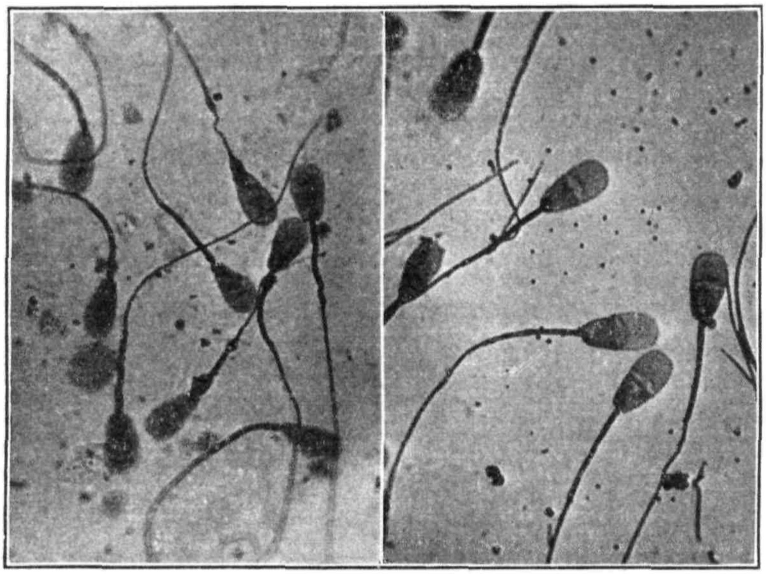

FIG. 64.—Abnormal and normal spermatozoa of bull. (*Courtesy Dr. W. W. Williams.*)

The amount of semen ejaculated by males varies both in quantity and quality between individuals, species, and seasons, and is influenced by the system of management and feeding. The color and consistency of semen varies between species and, when abnormal, such sires should be withheld from breeding. Spermatozoa should show progressive movement when examined microscopically in a hanging drop, and their number should be within the normal limits for the species. Their morphology, too, should be normal with not more than 15 to 20 per cent showing abnormalities in form, for there seems to be a general positive correlation between the percentage of abnormal sperms and low fertility or sterility, due regard being given to season of the year, previous sexual activity, and method of collection.

If a male has served too frequently or has not had service for a considerable time, the number of abnormal spermatozoa will generally be

increased. If semen is secured for examination from the genital tract of a female, various vaginal detritus may render accurate diagnosis difficult. The inclusion of bacteria, pus, or other cell debris may indicate a diseased condition somewhere along the male genital tract. The hydrogen-ion concentration and the respiratory rate of sperm are very useful indicators of semen quality.

Normal reproductive activity on the part of any animal entails the mating of healthy vigorous parents, proper feeding and care of the dam through gestation, a safe delivery, and proper feeding of the newborn from birth to puberty. Unbalanced physiological states owing to faulty nutrition anywhere along this devious route will eventually exact their toll in lowered degrees of fertility.

In the female of breeding age, unbalanced physiological states owing to faulty nutrition or endocrine aberrations may be expressed as ovarian cysts, quiet heats, adhesive cervical seal, or the production of eggs of low viability, or other abnormal ovarian, uterine, or vaginal conditions.

Many high-producing cows exhibit only faint and short periods of estrus while milking heavily. This results in temporary sterility, for the heat periods usually return to normal when milk production declines. Although only temporary, this form of sterility is, nevertheless, very costly, for it results in too long a time between calvings with the consequent reduction in milk production as well as interference with the breeding program, which should be based upon the expectation of a definite number of cows freshening during each month of the year, as dictated by market requirements.

Males, when used for "heavy" service, need a good supply of nourishing feed rather high in protein to keep their reproductive glands properly stimulated. At other times, they should be fed with moderation and not allowed to get thin, nor should they be fattened excessively for show or other purposes if their breeding powers are still valued.

As heat approaches, the mucus secreted by the cervix should liquefy. This sometimes fails to occur, and the spermatozoa are unable to penetrate through the thick mucus of the cervix. At other times the cervix may be swollen and inflamed to such an extent that the spermatozoa cannot penetrate through to the uterus. In these and other similar cases, the prompt calling of a veterinarian will prove a profitable investment.

The corpus luteum persists in the mare for about one-half the gestation period. In other mammalian farm animals, it persists right through pregnancy and is absorbed subsequently. In some instances the corpus luteum persists more or less indefinitely and thus precludes ovulation, heat, and successful breeding. Manual dislodgment of the corpus luteum is generally followed in a day or two by abortion if the animal is

pregnant, or by heat if not pregnant. It would seem inadvisable generally, however, to breed animals at such heat periods. Rather one should wait until at least the next regular period, which should follow in 18 to 22 days. It occasionally happens also that the corpus luteum becomes cystic rather than being absorbed without the appearance of fluid. This is often accompanied by ovarian adhesions and sometimes by tubular inflammation.

Improper physiological functioning may, and no doubt often does, manifest itself as sterility. This is especially true of those dairy cows which make a huge record one year and then fail to breed for one or several years, or perhaps forever. Such animals, overstimulated with high-protein feeds, are almost literally burned out, and their period of useful-

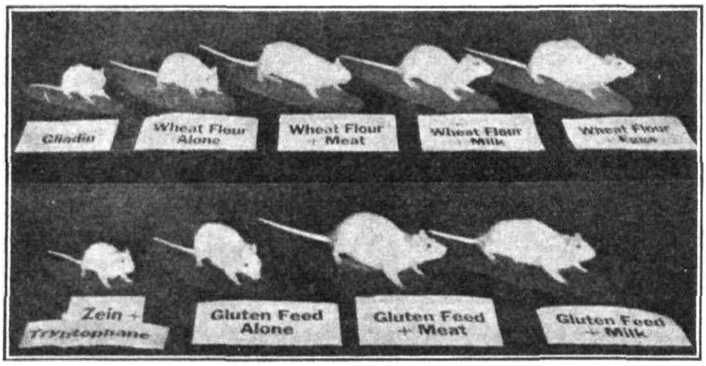

FIG. 65.—Showing the effects of different proteins in stimulating growth. All the rats in the picture were fed balanced rations. (*Courtesy of Drs. Osborne and Mendel.*)

ness shortened. They have also drawn heavily on the mineral reserves of their bodies and cannot be expected to function normally until these mineral reserves have been rebuilt. This rebuilding of protein and mineral reserves can usually be accomplished by an adequate dry resting period of at least 2 months before calving, together with liberal feeding of silage, leguminous hays, and a good grain mixture, such as 3 parts each by weight of hominy, wheat bran, and ground oats and 1 part of linseed-oil meal during this time.

The general and specific requirements of energy, proteins, minerals, and vitamins for normal reproduction have been discussed hitherto. One of the first things to be done if breeding troubles arise is to analyze critically the ration being fed and to determine whether there is any likelihood of there being a serious deficiency of any of these four necessary constituents. As is well known, the feeder-breeder's problem will be much simplified if he is feeding high-quality, properly cured leguminous hays.

A recent study of Lardy, Pounden, and Phillips[1] at the University of Wisconsin has shown that the vagina of the cow at anestrus has a pH of 6.4, that the cervical mucus passed into the vagina at heat has a pH of 8.33, and that the pH of the uterine fluid is of pH 6.8. They also point out the probable inefficacy of weak alkali or acid vaginal douches in the cow as far as effective sex control is concerned. Excessively acid or alkaline conditions of the vagina might be deleterious to the well-being of spermatozoa, though there is a fair possibility that difficulties of this sort might be obviated by artificial insemination. There is great need for more experimental work in this field.

Sudden changes in the feed and care of breeding animals should be avoided. Changes of feed or of surroundings are apt to induce abortion.

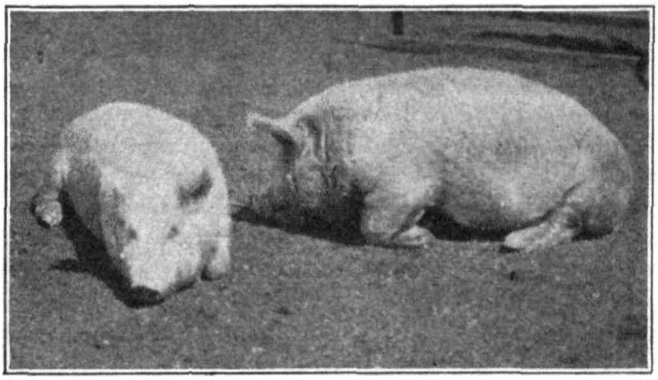

FIG. 66.—Pigs suffering from rickets because of a deficiency in lime and phosphorus or a deficiency in vitamin D or both. (*Courtesy of Wis. Agr. Exp. Sta.*)

If allowed free access to salt, pregnant sows not used to it are very liable to overeat, resulting in abortion. Any untoward event that upsets the physiological balance of a pregnant female is quite apt to result in abortion. Oftentimes, animals transported to foreign countries or animals imported into America are temporarily sterile until they become fully acclimated.

Traumatic Sterility.—Injuries to various portions of the male or female genital tract often cause sterility as do certain types of injuries to other portions of the animal's anatomy. Occasionally, young females are served by males of too great weight resulting in injuries to the pelvis. Although these injuries might not interfere with fertilization and normal embryonic development, they often do interfere with normal safe delivery

[1] LARDY, H. A., POUNDEN, W. D., and PHILLIPS, P. H., H Ion Concentration of Various Fluids of the Genital Tract of the Cow, *Soc. Expt. Biol. and Med. Proc.*, **44**, **517**.

of the young. At time of parturition, the uterus, cervix, or vagina may become badly lacerated, and, if this is followed by the invasion of harmful organisms, the breeding worth of the animal may be greatly reduced. Destruction of areas of cotyledons in the cow either through manual removal of the placenta or through the action of harmful organisms often results in a lowered degree of fertility. Injuries leading to various types of hernia or to uterine torsion likewise lower or destroy future breeding abilities.

In the male, injuries to the spine, pelvis, or hind legs or the occurrence of hernia may render him incapable of normal service. In such cases, artificial insemination might be resorted to, but the breeder must carefully consider the possibility of such a male's passing on his weaknesses to his offspring. Injuries to the exposed penis or testes may also result in sterility.

Pathological Aberrations.—A variety of invading organisms may render both males and females sterile. General systemic maladies such as tuberculosis, hog cholera, foot-and-mouth disease, rinderpest, etc. may lead to temporary or permanent sterility or cause females to abort, and the first-named disease may invade directly any portion of the genital tract of either sex, causing lowered fertility, sterility, or the appearance of tuberculosis in the young. In addition, tumors, either benign or malignant, may occur in any part of the genital tract, rendering service impossible or fertilization and normal embryonic development and safe delivery less likely.

In the male, inflammation of the testis (orchitis) is of fairly frequent occurrence. The testes become tender, swollen, and hot. The condition may be due to the presence of tuberculosis, Bang's, or various pyogenic organisms, and these conditions may be either chronic or acute. Orchitis may lead to a degeneration or blockage of the seminiferous tubules, from which recovery is impossible, or to an eventual hypoplasia of the whole organ. It hardly seems necessary to say that males showing any abnormalities of the testes should not be used in service.

The long, coiled epididymis (nearly 100 ft. long in the horse, according to Schmaltz) frequently becomes inflamed, and owing to its location it is difficult to differentiate from general orchitis. In fact, the two conditions often coexist. The causative factor in this derangement is not known, neither is any preventive or curative measure other than safe management and the conservative use of males on nothing but clean females. The vas deferens, except at the ampulla, is not often attacked by disease organisms, and whether this occurs other than as an accompaniment of disease of the seminal vesicles is unknown.

The seminal vesicles, which vary considerably in size in the various farm animals, often exhibit swelling, tenderness, and a general unhealthy

condition. The cause of this trouble is not definitely known, but the Bang's organism has been recovered from diseased seminal vesicles. Pus is often found under these conditions and, if the ejaculatory duct remains open, will be discharged with the semen. The vesicles may become abscessed, and this often breaks through into the rectum. Cure for this trouble is very difficult, if possible at all, when the condition becomes well established.

Inflammation of the prostate gland is not common in mammalian farm animals but is known to occur infrequently in old dogs. The bulbo-urethral, or Cowper's, glands are not known to be often diseased in farm animals.

The penis of the male, together with the prepuce or sheath, is a likely seat of infection that may lower fertility, pass on the inflammation to the females which he serves, or, if severe, make copulation impossible. This is particularly the case with vesicular venereal disease, and ruminant males and boars often show the nodules of infectious vaginitis. Collections of the exudate from the penis often harden within the sheath causing irritation and sometimes bleeding following service. If service seems painful to the male or swelling of the sheath becomes evident, steps should be taken to wash out the sheath with mild antiseptics.

Males are purchased and retained merely for the purpose of viable germ cells that they can deposit in the female genital tract. Any condition that renders this service impossible or involves the spreading of disease through the females in its accomplishment renders the male worthless or perhaps a distinct liability. Young males, therefore, should be purchased only from clean herds, and older males should be subjected to a thorough clinical and laboratory examination before their induction into any herd or flock. Better buy a few bad genes in a healthy body than a few good genes if these must necessarily be delivered in a diseased body. Certain types of genital diseases cannot be detected by physical or laboratory diagnosis, and the only sure method of detection is the use of the male on a few females. If the females become pregnant and show no evidence of disease, the male can be used with a fairly high degree of safety.

In the female, any part of the genital tract may become diseased or injured in such a way as to render the animal sterile. As in the male, the whole tract behaves as a unit; infection in one part may spread to another, making it difficult or impossible to determine the original site of infection. For healthy, vigorous offspring a normal female genital tract is the first necessity.

The ovary of the female is less exposed to injury than the testis of the male, although it is exposed to any abnormal condition that might arise in the peritoneal cavity. Uncomplicated ovaritis in mammalian

farm animals is rare, according to Williams, although adhesive inflammatory conditions involving both the ovary and the infundibulum of the oviduct have been observed. Most of the follicles that start to develop in the ovary are arrested and become atretic or atrophy. This condition seems to be normal, only becoming abnormal if all the follicles follow this course.

Occasionally a follicle grows to maturity but does not rupture in due time. This leads to the continued production of fluid in the follicle and causes the condition known as *nymphomania* (sexual insanity). The ripening of a follicle brings the animal in heat; its persistence makes heat more or less permanent. Such animals are known as *bullers*, for they are more commonly found in cattle, but the condition is known in other species. Animals so affected are highly nervous, seek and accept the male at all times, and are infertile because the egg does not rupture from the ovary and cannot, therefore, become fertilized. The follicle, in other words, becomes cystic—overdistended with fluid. A usual accompaniment of this disorder is a continued related condition of the pelvis, its tilting backward and downward and the elevation of the posterior region of the spine and raising of the tail. The exact cause of the condition is unknown, but it is thought to be due to impaired endocrine functioning. The immediate condition can be cured by manual rupture of the cystic ovisac per rectum. When this is done, however, the animal should not be bred until it has passed two or three normal heat periods.

Nymphomania usually sets in quite suddenly but is often preceded by a series of irregular heat periods often of longer duration than usual. Like many other reproductive disturbances, this one is not likely to be severe if noticed and treated early. This again emphasizes the necessity for the breeder, whose animals are confined, to keep careful records of heat periods. Females suffering from nymphomania show the normal reactions of heat, bellowing, nervousness, sexual mimicry, etc., usually to an exaggerated degree. In extreme cases, the only cure is ovariectomy. A reduced form of nymphomania is very occasionally caused by central ovarian cysts that do not protrude from the ovary and can only be removed surgically.

Inflammation of the oviducts, called *salpingitis*, is not known to be caused by any one organism. These infections are thought to be secondary to diseased conditions of the cervix or uterus. They may be a simple inflammation, or the tube may become filled with fluid sometimes containing pus. The condition can only be determined by rectal palpation or by insufflation of the tubes. Animals suffering from this trouble are practically invariably sterile, and cures are very difficult to achieve.

If the condition is prevalent in only one tube, this might be successfully removed through a laparotomy.

The uterus of the female is a likely host to a great variety of harmful organisms that may find their way there at time of service, parturition, or through the alimentary tract. Probably the most important, though not the sole, organism involved in inflammation of the uterus is the organism of Bang (bovine brucellosis). Both chronic and acute metritis are more likely to be found in herds positive to the Bang's disease agglutination test. In some cases the uterus becomes filled with a serous fluid, at other times with pus. Metritis severely lowers or entirely inhibits fertility. If diagnosed early, before irreparable damage has been done to the lining epithelium or cotyledons, cures may be effected. This involves siphoning off the uterine fluids, douching, perhaps rectal massage, and certainly sexual rest until the organ returns to normal. Heifers before breeding sometimes evidence fluid distention of the uterine horns and inflammatory conditions. For maximum breeding efficiency, therefore, heifers and fillies should be thoroughly examined per rectum previous to their first breeding. All females in a herd or flock should be watched for the type of their vulval discharge, especially at heat. Dairy cows that have calved without difficulty and have cleaned normally should, nevertheless, be examined for ovarian and uterine normality previous to their next breeding.

Retention of the placenta following parturition is often followed by metritis, which needs care and treatment at regular intervals in order that the tissues may be brought back to normal as quickly as possible. With the best of care and thoughtfulness some uteri will too early lose their functional power; without such care the breeder invites disaster.

The cervix, which is but a continuation of the uterus, forming its portal, is likewise subject to many disorders. Owing to its structure, inflammation of the cervix (cervicitis) is especially hard to treat and to cure. Except at parturition, the cervix is rather tightly closed and is thrown into many folds and crevices. It is, therefore, practically impossible to bathe all parts of this organ with antiseptic. The cervical canal can be examined by means of a dilator, and in the case of very valuable breeding animals amputation of part of the cervix may be attempted with good likelihood of success. Cervicitis and metritis generally coexist and usually result in complete sterility.

The vagina and vulva of females sometimes become highly inflamed owing to invading organisms, resulting in vaginitis and vulvitis. This is often accompanied by pus in the vagina. This organ is readily accessible and can be easily douched. The primary danger here is that the infection may spread forward to the cervix, uterus, or tubes if not

early detected and cured. These aberrations may be of either an acute or chronic nature and may be caused by a variety of pathogenic organisms. The old adage that "the eye of the master fattens his cattle" might well be paraphrased to read, "the eye of the breeder preserves the health of his animals."

Some men can walk through a barn or into a field and notice nothing irregular, whereas others would notice a dull eye in this animal, indicating perhaps the beginning of a digestive upset, or a suspicious discharge from that vulva, indicating the beginning of a genital upset. One of the main differences between successful feeders and breeders and the average men of these classes is just this ability to observe a little more closely. Observation must, of course be followed by examination, interpretation, and suitable action to obviate whatever difficulty presents. "A stitch in time saves nine" is nowhere so applicable as in the realm of the maintenance of both general and genital health in our breeding animals.

Abortion is the term applied to premature stillbirths. There are, in general, two sorts of abortion; one caused by injuries, improper feeding, or other things extraneous to the uterus; the other caused by microorganisms that invade the uterus, *e.g.*, the bacillus of Bang (*Brucella abortus*).

This latter type of abortion is a moot subject to which many investigators have assiduously devoted themselves, but even yet there remains a great deal to be learned concerning it. It is commonly spoken of as *contagious* abortion. There may be many organisms, capable of being spread from one animal to another, that are able, by their growth, to break down the delicate connections between mother and embryo at the placenta, thus paving the way for premature birth. This is a problem which veterinarians alone are trained and fit to handle, and any breeder having trouble from this cause will do well immediately to enlist the assistance of the best veterinarian available, but the breeder himself should aid by carefully observing, cooperating, and carrying out the veterinarian's suggestions, as well as by individual study and thought.

Both the complement-fixation and the agglutination tests are used to determine whether animals are positive or negative regarding Bang's disease (contagious abortion). In many states of the United States, provision is made by the state for carrying out gratis the laboratory technique involved in making the blood test for Bang's disease. The breeder, of course, must arrange to have the blood samples drawn. It would be advisable for every breeder to get an occasional blood test on every animal in his herd. With this information at hand, he is much better able to safeguard the health of his herd. If the test shows that he has two or three positive animals, these can be watched more closely at parturition, and under most conditions it would be possible to at

least partially isolate them just previous to calving and as long thereafter as they showed any discharge from the vulva. Experience has shown that Bang's disease is most apt to be spread to other animals at time of parturition and during the following few weeks. All positive cows should be kept away from the clean members of the herd at this time.

Many dairy-cattle breeders have eliminated Bang's disease from their herds by a system of test and slaughter similar to that used for the elimination of tuberculosis. Many states and the Federal Government have been paying indemnities for such positive animals when slaughtered during the past several years.

Other breeders have tried to control the ravages of this disease by a variety of means. Since 1910, the Bureau of Animal Industry has been working with bacterins, immune serums, and vaccines.[1] The first two proved worthless. Vaccines of various potencies have been used, the most virulent generally being found best but having the very serious disadvantage of the organism becoming localized in the udder so that the animals become chronic carriers and capable of transmitting the organism to man through their milk.

Drs. Schroeder, Cotton, and Buck of the Bureau of Animal Industry had worked with various avirulent strains of *B. abortus* for many years. In 1925, Dr. Buck began experimenting with the vaccinating of four- to six-month-old calves by means of a virulent strain. These calves, although heavily exposed during their first pregnancy, did not abort.

Later, Drs. Buck and Cotton began to experiment with an avirulent strain (No. 19) for calfhood vaccination, again with very marked success. This prospect was so promising experimentally that it was decided to give it a trial in the field. From 1936 to 1940, some 17,000 calves in 260 herds located in 24 states with an average of 29.2 per cent positive and 8.4 per cent suspicious cows per herd (more than 15 per cent positive) were vaccinated with strain No. 19 organisms. Out of a total of 8,182 calvings (5,673 first calvings; 2,026 second calvings; 483 third calvings),

7,892, or 96.2 per cent, had normal parturitions.
6,526, or 82.9 per cent, of those calving normally were negative.
947, or 12.0 per cent, of those calving normally were suspicious.
399, or 5.1 per cent, of those calving normally were positive.
310, or 3.8 per cent, aborted.
182, or 58.7 per cent, of those aborting were negative.
29, or 9.3 per cent, of those aborting were suspicious.

[1] This discussion of calfhood vaccination is based on a report by Drs. J. C. Mohler, Chief of the Bureau of Animal Industry, A. E. Wright, and H. H. O'Rear, of the Bureau of Animal Industry, to the U.S. Livestock Sanitary Association at Chicago in December, 1940, and reported in *Hoard's Dairyman* for Jan. 10, 1941.

99, or 31.9 per cent, of those aborting were positive.
128, or 1.6 per cent, of the total 8,182 calvings following calfhood vaccination were presumably due to *B. abortus*.

The report of Dr. Mohler *et al.* gives the following warning concerning the use of calfhood vaccination.

In considering the potential possibilities of *Brucella abortus* vaccine in the control and eradication of this malady, it should be readily recognized as a procedure that is not sufficiently simple in application to withstand promiscuous usage, and if viewed solely on a basis of simplicity, disappointment and disaster are bound to follow in its wake. Consequently it is apparent at this juncture that a warning should be sounded against any over-enthusiastic tendencies which obviate or subordinate cardinal principles that are of fundamental importance in a procedure of this particular type.

Exacting rules and regulations will be required to govern its use, and a definite plan must be adopted with respect to the physical application of these principles, in addition to a close supervision of the preparation of the product, if any major degree of success is achieved and complications which tend only to confuse the situation are to be avoided . . .

Dairymen who seek the vaccination of their adult cattle with or without the vaccination of their calves should be warned that the number of city and town health officers who are requiring milk from non-reacting cattle for their citizens is constantly on the increase. Too frequently have we learned that such owners have been deprived of their markets because their vaccinated cows had continued to react following vaccination.

Moreover, regulations in a number of states require that cattle destined to such states must not be reactors to the blood test. Therefore, shippers of both dairy and beef cattle should be properly advised against promiscuous vaccination without supervision before they risk shipments in violence to the regulations of the state at destination.[1]

The other type of abortion is usually spoken of as *sporadic* abortion. These cases usually occur singly because of some untoward happening to one or possibly a few animals, but they are not due to an infectious organism. They may be grouped under the following headings:

1. Injuries.
2. Mismanagement.
3. As an accompaniment to an acute feverish disease.
4. Poisoning.
5. Unbalanced physiological states.

An injury severe enough to cause abortion will probably leave external marks as evidence that some such thing has happened. Slipping, crowd-

[1] *Hoard's Dairyman*, pp. 20 and 31, Jan. 10, 1941.

ing through narrow doorways, or being kicked by other animals or generally maltreated by caretakers will often cause abortion, and in some of these instances it is difficult to see external evidence of what has transpired.

Mismanagement, such as putting mares at hard, jerky work, is sometimes a cause of abortion. Anderson reports a case of a mare that had been bred but was not thought to be pregnant being served again by a stallion and aborting a few hours later. He calls this an *induced* abortion.

Abortion, which is an accompanying phenomenon to an acute feverish disease, will generally be recognized as such owing to the presence of the disease.

Any poisonous substance that an animal eats or drinks might cause abortion. Ergot, a fungus disease of some plants, has a powerful stimulating effect on the uterus and may cause abortion. Symptoms of poisoning are usually very noticeable and should be readily recognized.

Unbalanced physiological states due to faulty nutrition no doubt cause many abortions. This is particularly true with animals that are hard-worked, *e.g.*, cattle making large milk and fat records. Such animals often have to draw on their own body substance for materials not sufficiently supplied in their rations. This may be especially true of minerals, such as calcium and phosphorus. At any rate, the feeding of minerals has been followed by a cessation of abortion in many dairy herds.

Any animal that is not in a normal state of productive and reproductive health should be removed from other animals in order to lessen the danger of spreading possible contagious disease. If trouble arises, it is well to seek the advice of a competent veterinarian. It is unfair to delay overlong before seeking such advice and help and at the same time to expect the veterinarian to perform miracles. Abortion, both sporadic and contagious, costs breeders millions annually. Proper thought and quick action can lessen these losses considerably.

Managerial Influences on Sterility.—The advantages gained by the acquisition of desirable germ cells can often be vitiated or lost through poor management of the breeding herd or flock. This is one of the most important considerations in the whole field of breeding. Care must be used in searching for the cause of breeding difficulties in order that simple, almost obvious causes be not overlooked in the attempt to locate the trouble in something more complex. The matter of lack of exercise, simple enough in itself, causes untold breeding losses yearly. Without a certain amount of exercise, it is impossible to keep an animal in first-class physical condition, and it is likely that, if the animal is in poor general condition, it will be producing nonviable or weak spermatozoa or ova.

To cite a common example, it used to be the practice to drive or ride a stallion over a large area each spring, serving mares at the various farms en route. These stallions were notedly sure "foal getters," averaging 80 to 90 per cent or better. Now practice has changed, mares usually being brought to the stallion, and with this change has come about a marked decrease in the percentage of foals gotten by the average stallion to a point close to 60 per cent.

Part at least of this decrease is traceable to lack of exercise. Oftentimes the only thing necessary to change an impotent bull into a vigorous "sure" sire is to work him in a cart or on a treadmill, or in some other way ensure his getting exercise. A boar unable to serve successfully can often be brought back into usefulness by putting him out where he will get exercise and lose fat. It is sometimes necessary to drive him to his exercise daily. The same general conditions hold with rams. In successfully managing breeding animals, both males and females, exercise is a point that should receive weighty consideration if success is to be achieved. The matter of exercise or work can, of course, be overdone. It should be realized that with breeding animals one cannot demand full productive as well as reproductive returns at the same time. Reproduction requires energy, which must be subtracted from the amount ordinarily expected of animals not engaged in reproduction. As F. Hoesch has stated: "There is no gain in attaining great service from our animals without lasting maintenance of their health, but rather it is a loss for which it is difficult to compensate."

Another loss in breeding efficiency sometimes leading to complete sterility is the matter of the amount of service by males. When born, animals are sterile, because their reproductive organs have not matured and are not capable of producing viable spermatozoa or ova. Fertility makes its appearance at puberty. If carefully fed and handled, not used overmuch, and kept free from infection, a normal animal will remain fertile for many years, the exact period of life and usefulness being determined by (1) inheritance and (2) the rate at which the vital patrimony is spent. Eventually, of course, even though life persists, the power for procreation vanishes. Breed histories furnish examples of animals that have retained their breeding powers over very long periods. Any breeding animal should be kept in the breeding herd as long as it continues the regular production of vigorous offspring of high individual excellence.

Just as young animals should not be overworked in service before they have attained a certain amount of maturity, so old animals should have their breeding powers conserved through lightened breeding work. Valuable breeding dairy cows, after the age of eight or ten years has been attained, should be granted a somewhat longer rest period. Old mares, if their physical condition is at all questionable, should be allowed to

skip a year in dropping foals and everything should be done to keep valuable old breeding males serviceable as long as possible. These are matters of judgment on the part of the owner or manager, and such privileges are usually granted by those who appreciate somewhat the strain involved in continued reproduction, often asked in addition to some productive work.

Good management also calls for service by the male away from his usual stall or pen in order to lessen the likelihood of the development of wasteful habits such as masturbation.

Good management involves the supplying of whatever feed ingredients are necessary for the type and amount of production and reproduction that are being demanded. It also involves breeding at the proper time during heat to best guarantee success, as well as some attention to the likelihood of viable spermatozoa being deposited by the male. This, of course, is influenced greatly by the amount of prior service the male has given. It involves the first breeding of females at such a time that their own growth and production will be adequately cared for as well as the probable vigor of their offspring. Good management involves an appreciation of the balance that must be maintained between production and reproduction, especially, of course, in mares and cows, and a realization that too great a draft on one of these phases generally means injury to the other. It means too that certain types of demands such as hard, jerky pulling are not to be asked of pregnant mares. Reasonable comfort, cleanliness, and protection from the elements are also involved in good management. Breeding females, especially, are delicately adjusted organisms whose needs, capabilities, and limitations must be understood in a broad sense if a breeder is to achieve success and avoid the pitfall of lessened fertility or complete sterility.

In short, it can probably be said safely that most variations in fertility are due to management. If your herd or flock is not reproducing at an efficient level, don't be too anxious to pass the buck to inheritance, to hard luck, or to the animals themselves. The fault is more than apt to lie with your management, and it may lie in some comparatively simple thing that you are overlooking.

Summary.—In this chapter we have tried to catch a broad glimpse of the manifold factors that influence the fertility of our animals or may cause sterility. Their number, as we have seen, is almost legion and there seems to be no necessity to recapitulate all of them at this point.

The breeder's task would seem to be that of selecting his breeding animals from naturally fertile strains; of feeding and managing mature males and females so that viable healthy germ cells may be produced; of growing out his young stock in a sanitary environment and on suitable, complete rations; of attempting to strike an intelligent balance between

production and reproduction; of setting all the barriers possible between his animals and injuries or organisms that might lower their breeding efficiency; of keeping accurate records of all matters pertaining to breeding health and efficiency, so that he may know at all times where he stands and in what direction he may be heading.

Finally, it hardly seems necessary to warn against putting our faith in some cure-all of doubtful efficacy and thereby delaying the real job of securing professional service, thus allowing some malady to get a firm foothold. Such a policy is the best possible example of being "penny-wise and pound-foolish."

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CHAPTER XI

ARTIFICIAL INSEMINATION

by

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Few topics have been as widely publicized or as readily accepted by livestock breeders during the past decade as artificial insemination. Artificial insemination is, by definition, the deposition of spermatozoa in the female genitalia by artificial rather than by natural means. The successful application of this method of breeding depends upon an understanding of four fundamental problems: (1) the collection of semen from the male; (2) the treatment or preservation of the semen prior to its use; (3) the deposition of the semen in the proper region of the female tract; and (4) knowledge of the physiology and pathology of the genital organs.

History of Artificial Insemination.—Artificial insemination is not new. Loessl (1934) relates a supposedly authentic account of an Arab chief in 1322 who mated a prized mare with the stallion of an enemy chieftain by stealthily collecting semen from the stallion's sheath and successfully artificially impregnating his mare. It is definitely known that Spallanzani was successful in the artificial insemination of dogs in 1780, and Hunter (1799) produced a pregnancy in the human by this method. Iwanoff, a Russian physiologist, began a study of artificial insemination in farm animals as early as 1899, established a laboratory for further investigation in 1909, and initiated large-scale investigations and the application of the findings in 1922. During the past 10 years, scientists and technicians in all parts of the world have undertaken work in this particular phase of reproductive physiology. In 1938 it was reported that 5 per cent of the cattle in Russia were artificially inseminated and that as many as 15,000 ewes were mated with a single ram during one breeding season.

The first artificial-insemination association in the United States, a group of 102 dairymen owning 1,050 cows and organized for their mutual benefit, was established in New Jersey in May, 1938, and was so enthusiastically received that two others of similar size were organized in the same state in the fall of that year. Artificial insemination had been successfully used by horsemen in this country for many years, but not as extensively or successfully as by the present-day artificial-insemination associations. A summary made in 1940 by the National Dairy Products

Corporation showed that approximately 50,000 cows owned by 4,000 to 5,000 dairy farmers in 22 states were enrolled in 54 artificial-insemination associations. Groups in many other states are in the process of forming similar organizations, and it is conservatively estimated that nearly 100,000 dairy cattle, in addition to other classes of farm animals, were artificially inseminated in 1941.

ADVANTAGES OF ARTIFICIAL INSEMINATION

Increase Use of Good Sires.—The greatest advantage of this method of breeding is that it will increase the usefulness of superior sires. Proved sires, whose ability to transmit desirable characteristics is known, can be mated with many times the number of females that would be possible under natural conditions. It has been reported that one bull was mated with about 900 cows during a single year in a Danish breeding society, and a Russian worker reports the insemination of 15,000 ewes with the semen of one ram during a single breeding season. The small-herd owner can, by this method, avail himself of the services of sires formerly available only to the owners of large herds, for when the purchase and maintenance costs of a valuable sire are distributed among a large number of members of an artificial-insemination association, the average service fee is small ($5 per cow in most associations).

Allow More Sires to Be Proved.—Sires can be more effectively proved in artificial-insemination associations. Many sires are never proved, and others have been destroyed before their worth has become known, because the size of the herds in which they were used was small. Males that are mated with several hundred females during a single year offer the geneticist opportunities for prediction which have formerly been denied. Members of breeding associations should consider as an essential part of their program the proving of a few promising young sires. When members breed only a few females to an outstanding young sire, they distribute the risk of possible failure but greatly multiply the opportunities of proving sires at an early age. If this program is followed, we may expect an entirely new concept of what a proved sire is, and we may rightfully expect him to have 100 quality daughters rather than 5 or 10.

Lessen Disease.—The danger of spreading genital diseases is reduced. Artificial insemination, when carried out on a large scale, should be in the hands of a specially trained veterinarian. His knowledge and experience will result in the prevention and early detection of genital diseases or abnormalities and the recognition of lowered fertility, which usually precedes sterility.

Overcome Physical Handicaps to Mating.—Artificial insemination is often of value in overcoming certain nonheritable physical difficulties. It facilitates the mating of animals of greatly different size; it extends the

usefulness of sires that for some reason may have become incapable of performing natural service; it increases the use of males of monogamous species such as the fox; and it promises to be a useful technique in hybridization experiments.

Creates Large Families of Animals.—Artificial insemination will tend to result in the development of large families of superior animals within particular regions. The end result should be not only the improvement of the various classes of livestock but the attraction of buyers from other regions when the uniformity of the families becomes evident.

DISADVANTAGES OF ARTIFICIAL INSEMINATION

Must Conform to Physiological Principles.—The enthusiastic reception of this form of breeding has, in many cases, led to the dissemination of false information concerning its usefulness. Some writers have led us to believe that females may be inseminated at any time during the estrual cycle, whether in heat or not, with semen collected many days or even weeks previously. Extensive studies of several thousand cows have shown that the average number of natural services per conception is 1.5 and that the same number are required when artificial insemination is used. With the exception of certain individuals with physical defects remedial by artificial insemination, females that consistently fail to conceive following natural service seldom become pregnant following artificial breeding.

Might Increase Spread of Disease.—The danger of spreading genital disease is greatly increased if this method of breeding is improperly applied. Carelessness or ignorance might result in the rapid spread of disease. Unfortunately, certain diseases of the reproductive organs cannot be detected by physical or laboratory diagnosis, and the final test lies in actual usage of the male. Sires of unknown or uncertain history should be mated with only a few females and then be withheld from service until the females are safely pregnant.

Practice Has Limitations.—The techniques of collecting and introducing semen have been highly developed, but the methods of extending the usefulness of semen for long periods of time need further study. The science of reproduction is not yet an exact one. The causes, prevention, and treatment of sterility are imperfectly understood, and systems of management that can be relied upon without fail for a particular individual or herd do not exist. In brief, the desire to artificially inseminate a cow in California with the semen of a bull in Massachusetts is not always brought to fruition. These facts must be considered as a disadvantage to the use of artificial insemination at the present time.

Various Abuses Possible.—The use of artificial insemination by unscrupulous operators might result in widespread damage. Trained

workers can detect differences in the spermatozoa of the bull, boar, ram, stallion, or cock, but even the most skilled would be unable to differentiate between the semen of an Ayrshire or a Holstein bull, to say nothing of the differences between two bulls of the same breed. If semen is transported from farm to farm, the care and character of the operator must be above reproach.

Restrict Bull Market.—The fact that the demand for poor or average sires will decrease if artificial insemination is widely adopted should probably be considered as an advantage rather than a disadvantage. The increased return that usually results from the use of outstanding sires should more than offset the loss from the decreased market for average males.

METHODS OF COLLECTING SEMEN

The ideal method of collecting semen is, theoretically, one which is completely satisfactory to the male, which is easy to use, which requires a minimum of equipment, and which permits the collection of a sample of normally ejaculated semen free from contamination with dirt, bacteria, or secretions from the female genitalia. Many techniques have been developed. Some methods are applicable only to certain species; others are too complicated in principle and practice; some do not result in the normal ejaculation of the male and the production of completely normal semen; and others yield semen that is diluted with vaginal and cervical secretions and often heavily laden with bacteria.

The Artificial Vagina.—During the past few years, Russian, British, and American laboratories have developed a type of apparatus called the *artificial vagina*. Its principle and construction, whether for bulls, boars, rams, or stallions, is simple, and it meets all the requirements of the ideal method. The apparatus is made up of an outer tube or casing, usually constructed of heavy rubber, metal, or one of the plastics, and an inner tube, or lining, of thin rubber. The space between the two tubes is usually filled with warm water or air or both; one end of the apparatus is open to allow the entrance of the penis and to the other end is attached a glass tube or beaker to catch the semen after ejaculation.

The success with which this method is used depends upon the skill of the operator and the training of the male, but most workers feel that it is the most satisfactory yet devised. The equipment should be clean, sterile, and dry before use. Males are very particular that the apparatus be of the correct temperature, pressure, and degree of lubrication, and conditions that suit one male may be unsatisfactory for a second. The proper temperature is attained by introducing warm water (40 to 45°C. for most males) between the outer and inner casings; the correct pressure depends largely upon the size of the penis of the male in question and is usually regulated by introducing or releasing air between the casings.

A small amount of lubricant, such as sterile mineral oil or white vaseline, should be applied to the first few inches of the inner rubber tube, but the amount used should be kept to a minimum, for it is undesirable to have any excess lubricant carried through the artificial vagina and mixed with the semen.

Males usually respond to this method without previous training. Best results are attained when the male is allowed to mount an estrus female and the penis quickly guided into the open end of the artificial vagina. If the proper temperature, pressure, and degree of lubrication have been maintained, ejaculation is instantaneous in the bull and ram

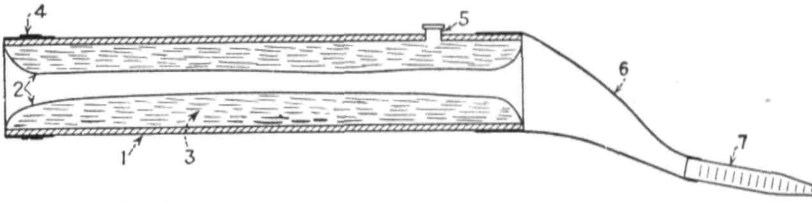

FIG. 67.—Diagrammatic artificial vagina for the collection of bull semen.
1. Outer rubber jacket.
2. Entrance for penis.
3. Warm water.
4. Heavy rubber band.
5. Water inlet.
6. Rubber cone.
7. Graduated test tube.

and is very shortly initiated in the stallion and boar. Active males may easily be trained to mount nonestrus cows, other males, or dummy females, and highly satisfactory samples of semen can quickly be collected.

The Massage Method.—Miller and Evans (1934) developed a technique of collecting semen from bulls by the massage of the ampullae of the vasa deferentia. The successful application of this method, which consists of the insertion of the arm into the rectum, the location and manipulation of the ampullae, seminal vesicles, and prostate region, and the collection of semen as it drips from the glans penis, requires a high degree of skill. It is most valuable for the collection of semen from bulls with injuries to their legs, backs, or reproductive organs but for genetic reasons should probably not be applied to bulls suffering from physiological disturbances preventing service that might be transmissible. This method does not compare in usefulness with the artificial vagina. There are marked differences in the response of individual bulls; the semen is often contaminated as it drips from the glans penis; the volume and concentration of semen obtained by this method is often less than by service into an artificial vagina; and the mixture of urine with the semen at the time of collection often kills the spermatozoa.

Burrows and Quinn (1935) perfected a massage method for the collection of semen from the domestic fowl and turkey that is widely and successfully used. The copulatory organ of the male can be protruded by manipulating the cloacal region, and the semen stored in the bulbous ducts can be pressed out by the thumb and first finger.

Recovery of Semen from the Vagina.—One of the older methods of semen collection is the recovery of semen from the anterior vagina following natural service. This can be accomplished by introducing a glass or rubber catheter into the vagina, locating the pool of semen, and aspirating it into a syringe. This method can be used satisfactorily for the recovery of stallion semen if scrupulous precautions are taken regarding the health of the females utilized as collectors, but even in this species it is not the most desirable technique. The simplicity of the method is overbalanced by the disadvantage that the semen becomes contaminated with the secretions of the female genitalia, and, in case of genital disease, offers an excellent way of infecting other females.

The Breeder's Bag.—This method has been satisfactorily employed by some stallion and jack owners for many years and has been discarded by others. The chief criticism of this method has been the fact that the bag often slipped from the glans penis at the time of withdrawal, but this difficulty has recently been overcome by the development of a longer type of breeder's bag. This method has the advantages of simplicity, low cost, and the recovery of uncontaminated semen, but it is applicable only to equines.

Electrical Ejaculation.—Gunn (1936) developed a method of collecting semen from rams by subjecting them to electrical stimulation in the lumbar region. This technique has been valuable from the research standpoint but has thus far been of limited practical value. The equipment is rather expensive, requires a high degree of skill to operate, and gives variable results even in experienced hands. Although it does yield semen samples with a minimum of contamination, its other disadvantages limit its use.

THE EXAMINATION OF SEMEN

The successful application of artificial insemination is, to a large extent, dependent upon the quality of the semen used, and those responsible for the collection and insemination of semen should be competent to estimate its condition and potentialities. Various methods of determining semen quality have been devised, but nearly all investigators and clinicians consider: (1) volume of semen (2) motility of the spermatozoa, (3) the number of spermatozoa per cubic millimeter, (4) the total number of spermatozoa in the entire ejaculate, (5) the number of abnormal sperm forms evident by a microscopic examination of a stained smear, (6) the pH of the semen, (7) the freedom of the semen from bacteria, protozoa, or debris, and (8) the duration of motility of the spermatozoa. The chemical composition of the semen, the amount of glycolysis, the buffering capacity, the oxygen consumption and carbon dioxide output, and the resistance of spermatozoa to certain unfavorable environments have

also been examined in semen studies, but their specific relations to fertility are not sufficiently clear at the present time to warrant their routine use.

Purdue University
Agricultural Experiment Station
SEMEN STUDIES

Date__________ Bull__________
Hour__________ Ram__________
Method of collection Stallion__________
__________ Boar__________
Cock__________

Morphology of Spermatozoa

Ejaculate number	Tailless	Coiled tails	Enlarged middle pieces	Middle-piece beads	Filiform middle pieces	Tapering heads	Damaged heads	Small heads	Giant heads	Double heads	Undeveloped sperm			Total abnormals per 1,000	Remarks

Hemacytometer count

	1	2	3	4	5	Total	Number per cubic millimeter	Volume	Total sperm	pH	Motility

FIG. 68.—Form used in semen analysis.

Volume of Semen.—As previously pointed out, there are marked species and individual differences in the volume of semen produced at each ejaculate. As a general rule, within species, males that produce large volumes of semen are more valuable than those which produce small volumes. It is highly desirable, although not always capable of achievement, that sires being considered for purchase should produce average or superior volumes of semen. (See Chap. IV for the characteristics of semen of farm animals.)

Motility of Spermatozoa.—The motility of the spermatozoa should be determined as soon as possible after collection of the semen. This should preferably be done before the semen temperature has dropped markedly

and may be accomplished by placing a small drop of thoroughly mixed semen on a hanging drop slide in a warm room or with the use of a stage incubator and a microscope. Various types of motility have been described, but the clinician usually distinguishes *rapid, progressive,* and *in place,* or *undulatory,* motility and scores semen samples on a basis of 0 to 5 in which:

5 = 80–100% progressive motility, swirling motion of the drop as a whole;

4 = 60–80% progressive motility, swirling motion indefinite or absent;

3 = 40–60% progressive motility, movement limited to individual spermatozoa;

2 = 20–40% of spermatozoa showing undulatory movement;

1 = 1–20% of spermatozoa exhibiting undulatory movement;

0 = no motility.

The presence of motile spermatozoa in semen has sometimes resulted in the improper diagnosis of fertility. It is now known that spermatozoa lose their fertilizing capacity prior to the cessation of motility, and whereas a semen sample containing no motile spermatozoa can be discarded as worthless, the presence of motility is not necessarily an indication of fertility. If a semen sample meets the requirements as far as volume, concentration, number of normal spermatozoa, etc., and exhibits a motility of 4 or 5, it is fairly safe to assume that the male is fertile.

Number of Spermatozoa.—The number of spermatozoa per unit volume of semen varies with species and individual, and breeding males should be expected to meet the requirements for their species as previously elaborated. Although only one normal sperm is required for actual fertilization, millions become lost or destroyed before they reach the vicinity of the ovum, *e.g.,* it is essential that stallion semen should contain about 60,000 and ram semen about 1 million spermatozoa per cubic millimeter if normal fertility is to result.

The number of spermatozoa in the entire ejaculate is obtained by determining the number per cubic millimeter and multiplying by the number of cubic millimeters of ejaculate. Spermatozoa counts may be made in several ways, but the simplest is by the use of the hemocytometer, following the same steps that are used in counting red-blood cells.

Number of Abnormal Spermatozoa.—Although Ham and Leeuwenhoek observed the spermatozoa of the human as early as 1677, it is only during the twentieth century that detailed studies of spermatozoa have been made. Williams and Savage (1927) made extensive studies of the morphology of bull spermatozoa and reported that in bulls with poor breeding records an average of 50.1 per cent of the spermatozoa were abnormal and that bulls with good breeding records averaged less than 16.6 per cent abnormal spermatozoa. These findings have been con-

firmed by Moench and Holt (1931), who found that men producing more than 25 per cent abnormal spermatozoa were of lowered fertility or sterile, and by McKenzie and Phillips (1934), who reported that normal rams produced not more than 15 per cent abnormal spermatozoa.

The determination of the number and types of abnormal spermatozoa in semen is considered an essential part of the complete semen examination at the present time, although there are considerable differences in the techniques used. Several slides of each semen sample to be examined should be prepared at the time of collection. This can be accomplished by placing a very small drop of thoroughly mixed semen at one end of a glass slide and drawing it out in a *very thin* film in the same way that blood smears are made. Considerable practice is required to make satisfactory slides of highly concentrated semen. The problem is one of obtaining a smear thin enough for study without mechanical damage to the spermatozoa. The slides may be allowed to air-dry and then may be placed in a saturated chlorazene solution for 5 to 10 minutes to remove mucus. They should then be rinsed in distilled water, washed in 95 per cent alcohol, allowed to dry, then stained with Ziehl's carbol-fuchsin for 1 to 2 minutes, rinsed in tap water, and allowed to dry. The stained slides should be studied under high-dry or oil-immersion objectives and classified by some definite scheme.

Nearly as many systems of classification as there have been investigators have been devised, but the abnormal sperm types most usually encountered are head abnormalities such as tapering, shrunken, large, or small heads; enlarged, beaded, broken, or filiform middle pieces; and coiled, broken, or missing tails. A study of a single smear of semen is sometimes misleading, for seasonal effects, excessive use, or long periods of sexual rest are among the factors that may temporarily increase the number of abnormal spermatozoa. McKenzie and Berliner (1937) in an extensive study of the reproductive capacity of rams found that, under Missouri conditions, the number of abnormal sperm forms increased during June, July, and August and were at a minimum during November, December, and January. Shropshire rams were more noticeably affected than Hampshire rams, the former having an average of 733 and the latter an average of 90 abnormal sperms per 1,000 during August.

Semen samples collected after prolonged periods of sexual rest should not be used for the determination of fertility. Spermatozoa that are not ejaculated tend to become senescent and are eventually broken down and resorbed. This fact often accounts for the failure of males to settle the first females to which they are bred at the beginning of the breeding season and must be taken into account in the estimation of fertility.

pH of the Semen.—The hydrogen-ion concentration of the semen tends to be rather constant for a particular species, and minor variations in

pH are usually of little significance. It is desirable that the pH of semen should be within the following limits.[1] Stallion semen is inclined to be slightly alkaline, 7.0 to 7.8, and ram semen is usually on the acid side, 6.2 to 6.8. Bull and boar semen vary from 6.5 to 7.5, although greater variations are not uncommon. As a general rule, semen that is slightly acid maintains its motility for the longest time, bull semen tending to be best preserved at a pH of about 6.75. Samples above 8.0 and below 6.0 are usually inferior in fertility.

Purity of Semen.—Semen should be collected and maintained as free of bacteria, cellular debris, dirt, blood cells, urine, or other foreign matter as is humanly possible. It is obvious that the presence of harmful bacteria, trichomonads, or other organisms or agents likely to result in genital diseases should be guarded against. There is no quicker way of spreading disease than by the widespread use of contaminated semen in artificial insemination. The contamination of semen with the secretions of the female tract is undesirable from the standpoint of genital health, but more undesirable because such contamination decreases the survival time of spermatozoa that are to be stored prior to use. Red- or white-blood cells, urine, water, soap, and other substances are toxic to spermatozoa and destroy or decrease their length of survival.

Duration of Motility.—The determination of the length of survival of spermatozoa under a particular set of conditions is one of the most accurate methods of estimating fertility but often requires excessively long periods of time to complete. A sample of whole bull semen that, when stored at 6°C., maintains its motility for 20 days is superior to a sample stored under the same conditions which remains motile for 10 days. Weisman (1941) has shortened the necessary time for observing the survival of human sperm by increasing the storage temperature. He reports that normal spermatozoa stored at 20 to 23°C. (room temperature) should remain motile for at least 24 hours and that at 37.5°C. (body temperature) for at least 10 to 12 hours. Weisman has found that human spermatozoa which do not survive at 45°C. for 1 to 2 hours are usually of poor quality.

ARTIFICIAL INSEMINATION IN PRACTICE

The Storage and Shipment of Semen.—The problem of maintaining the fertilizing capacity of semen during storage and shipment is one of the most vital in the successful application of artificial insemination. As previously pointed out, spermatozoa are sensitive to the action of temperature, light, pH changes, foreign substances of many types, and the ravages of time itself. Temperature shock should be avoided. All

[1] See LAMBERT, W. V., and MCKENZIE, F. F., Artificial Insemination in Livestock Breeding, Table 3, p. 36, *U.S. Dept. Agr. Cir.* 567, 1940.

utensils with which semen is to come in contact at the time of collection should be approximately at body temperature. If the semen is to be used for immediate artificial insemination—up to 1 to 2 hours—it may be kept in a tightly stoppered vial, in a dark place, at room temperature. If it is to be used at a later time, it should be slowly cooled at the rate of about 1°F. per minute until the final storage temperature of 3 to 8°C. has been reached. Semen that is too rapidly cooled is apparently permanently injured. Semen that has been stored at low temperatures should be gradually warmed prior to insemination, for optimum results, although practical experience has shown that warming prior to use is of less importance than the gradual cooling prior to storage.

Walton and Edwards (1938) and others have demonstrated that spermatozoa consume oxygen and produce carbon dioxide, but the significance of these findings has not, as yet, been fully agreed upon. It is fairly well agreed that the elimination of excessive amounts of air space in storage vials by placing a layer of pure neutral mineral oil over the semen is desirable. This tends to decrease the activity of the spermatozoa and thus to increase their longevity. Numerous reports on the effects of various nutrient media in prolonging sperm life have been published but there is considerable variation in the findings. Lambert and McKenzie (1940) have reviewed the more significant research relating to farm animals, and the reader is referred to their paper for a discussion of the subject.[1] Phillips and Lardy (1939) have developed a dilutor, or pabulum, for the preservation of bull spermatozoa that has been widely adopted in artificial-insemination associations and has been of definite value in prolonging the fertilizing capacity of bull semen. Their yolk-buffer medium is made up of a buffer consisting of 0.2 g. of KH_2PO_4 and 2.0 g. of $NaHPO_4.12H_2O$ per 100 cc. of sterile redistilled water, and fresh egg yolk. Equal amounts of freshly mixed buffer and fresh egg yolk are mixed, adjusted to a pH of 6.75, and then added to freshly collected semen in the ratio of 1 part of semen to 3 to 4 parts of yolk buffer. Semen treated in this manner has produced regular pregnancies at the end of 150 to 180 hours, and, in a few cases, after 10 days of storage.

For shipment,[2] semen should be placed in a clean glass vial with as little air space as possible between the semen and the stopper. This vial should be wrapped in dry absorbent cotton, placed within a second glass container, and sealed. The semen receptacles should then be wrapped in cotton and surrounded with chipped ice, care being taken to place additional layers of cotton at the bottom and top of a vacuum bottle to

[1] *Loc. cit.*

[2] The methods of preparing semen for shipment are described by Lambert and McKenzie, *loc. cit.*

eliminate excessive movement and breakage during shipment. Properly packed semen will maintain a temperature below 10°C. for 24 to 36 hours.

There are many misconceptions as to the length of time semen may be kept prior to use. Phillips at Wisconsin and Salisbury at Cornell[1] have reported that a limited number of cows have conceived with semen stored 10 days. Winters *et al.* (1938) reported the conception of two ewes with ram semen stored 6 days; McKenzie, Lasley, and Phillips (1939) produced pregnancy in swine with semen stored 56 hours and in the mare with 20-hour semen that had been shipped from Beltsville, Md., to Miles City, Mont. These storage periods are the maxima that have been achieved at the present time and are exceptional rather than the rule. For every sample of bull semen capable of inducing pregnancy at the end of a 10-day storage period, there are dozens of samples worthless at the end of 4 to 5 days. It is evident that there is considerable need for research in this field before we can expect widely separated animals to become impregnated at their owners' wills.

Insemination of the Female.—The insemination of the female is in most cases a simple operation involving the preparation of the technician, instruments, and the female, and the final deposition of the semen in the proper region of the genitalia. Under natural conditions, the male and female have little regard for asepsis, but it has been demonstrated beyond doubt that when natural processes are interfered with, whether by manipulation, surgery, or other means, the application of practical aseptic methods is advisable.

All instruments used for artificial insemination should be thoroughly washed, freed of *all* traces of soap, sterilized by heat or ethyl alcohol treatment, and should be absolutely dry at the time of use. The hands of the operator should be *scrubbed* free of all visible dirt, washed in 70 per cent alcohol, allowed to dry in the air, and, if possible, covered with sterile rubber gloves. This is essential if the hand is to be inserted into the female tract, as is usually done in the case of the mare, but is desirable in all classes of livestock. The female should be prepared for artificial insemination by washing the external genitalia with warm water and castile soap, followed by a thorough rinse with warm water alone. The lips of the vulva should then be spread and wiped with a piece of absorbent cotton to prevent dirt and debris that accumulate near the orifice from being carried into the anterior vagina. The semen that is to be used should have been gradually warmed to body temperature while the female was being prepared for insemination in order that the operator's time may be conserved.

The amount of semen required varies with the species and with the individuals concerned. If the concentration of spermatozoa per unit

[1] Personal communications.

volume of semen is low, larger volumes will be required, and multiparous females should be given more semen than young females because of the larger area of uterine tissue that must be traversed. Sows are usually inseminated with 50 to 100 cc. of semen, mares 20 to 30, cows 0.5 to 1.5, ewes 0.1 to 0.2 and hens 0.1 cc.

The type of instruments used for insemination varies with the species and the choice of the operator. Mares can be readily inseminated by pouring the required amount of warmed semen into a gelatin capsule

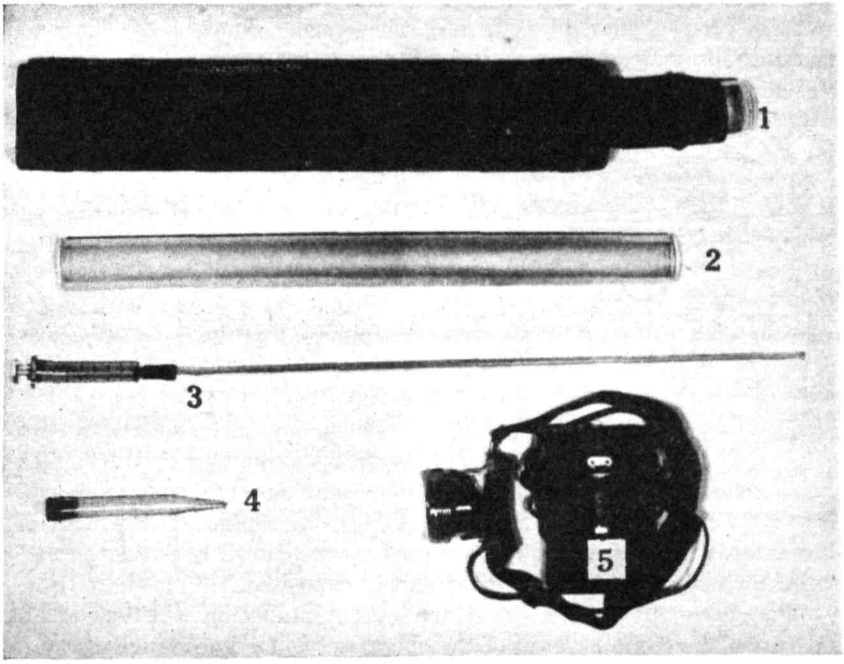

FIG. 69.—Equipment for the artificial insemination of cattle.

1. Artificial vagina.
2. Lucite or glass speculum.
3. Inseminating tube and syringe.
4. Graduated test tube.
5. Head lamp.

(1-oz. size) and quickly depositing the capsule well forward in the cervix by means of the hand. The gelatin quickly melts and the spermatozoa move through the uterus and into the fallopian tubes. Some workers prefer the use of a syringe and catheter. When this method is used, the cervix is brought into view by the use of a vaginal speculum, a glass or plastic catheter is guided into the cervix, and the semen slowly expelled into the uterus by pressure on the syringe. This method has the disadvantage of exposing the vagina and cervix to the environment during the operation and affords an opportunity for microorganisms to enter the genitalia.

Sows can be inseminated by means of a syringe and catheter without the use of a speculum. The catheter is introduced into the anterior vagina and, if the sow is in full estrus, can usually be worked into the cervix by careful manipulation. Since a large volume of semen is usually used for the sow, it should be very slowly introduced, taking care that none is lost from the vagina.

Cows are usually inseminated by means of a catheter, which is introduced either with or without a speculum. Most workers bring the cervix into view with a speculum, guide the catheter into the cervix until resistance is met, and slowly deposit the semen. Some of the clinicians carrying on artificial insemination on a large scale grasp the cervix per rectum with one hand and manipulate the catheter into it without a speculum. This method has the advantage of eliminating the necessity of carrying sterile specula for each cow and of reducing the chances of vaginal infections from environmental sources.

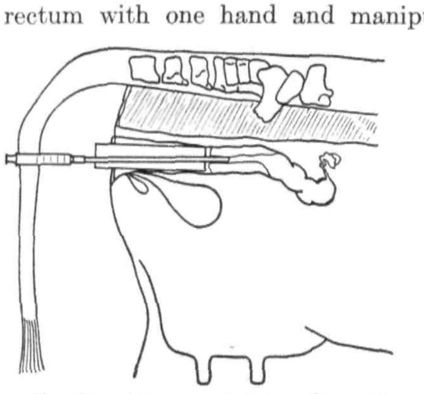

FIG. 70.—Diagram showing the equipment and technique used for the insemination of the cow.

Sheep are nearly always inseminated by the use of a catheter and speculum used in the same way as described for cattle.

Hens are inseminated by protruding the oviduct by the application of pressure in the cloacal region. A 1-cc. tuberculin syringe is introduced into the everted oviduct, pushed forward until resistance is met, withdrawn slightly, and the semen slowly deposited.

The successful application of artificial insemination will depend not only upon the technical skill of the operator but his knowledge of reproductive physiology. Insemination should be timed to coincide with ovulation; animals with prolonged estrual periods, *e.g.*, the mare, should be inseminated more than once during heat; species and individual differences in semen production should be recognized and adequate amounts of semen used; semen must be carefully handled during collection, storage, and insemination; and the importance of the relations between age, breed, season, nutrition, genetics, pathology, management, and fertility and sterility must be understood.

Organization of Artificial-insemination Associations.—Since the organization of the first cooperative artificial-insemination association in the United States by a group of New Jersey dairymen in 1938, interest in the movement has spread rapidly, and it is likely that similar organizations will soon be operating in nearly all states. Unfortunately, the overenthusiasm of some groups has led to the hasty establishment of

poorly organized associations, which have failed to function as expected, and it would seem advisable to discuss some of the factors affecting the success of such cooperative ventures.

The Sire Committee of the Extension Section of the American Dairy Science Association has been studying this problem since 1938, and their recommendations may be obtained in detail from the dairy-extension specialists of the various state colleges and universities.

Groups interested in the organization of artificial-insemination associations should conduct a number of preliminary meetings at which competent men outline the advantages, disadvantages, and limitations of artificial insemination. If the interested parties have a grasp of the problems involved, have no misconception as to the results that may be expected, and are still interested in a cooperative endeavor, specific steps can then be taken.

The prospective members should elect a board of directors who have sufficient knowledge and ability to manage such an association. A constitution and by-laws should be drawn up (or that suggested by the Dairy Science Association adopted) and agreed upon by the members. The duties and privileges of the members, officers, and employees should be clearly set forth. There should be no doubt as to the eligibility for membership, the methods of selecting, purchasing, and using sires, the membership and service fees, the health standards of the sires and cows, the system of record keeping, and the salary and duties of the veterinarian employed to perform the work.

Although a given set of rules cannot be expected to apply to all conditions, it has been shown that the most satisfactory results have been obtained:

1. When about 1,200 cows of a single breed are located within a 20-mile radius.
2. When work with not more than two breeds is initiated.
3. When the membership fee is adequate to provide for the purchase of outstanding sires and sufficient equipment to carry on the work.
4. When the veterinarian in charge has been specially trained in reproductive physiology.
5. When the bulls are properly managed and not overworked.
6. When a few promising young sires are proved for future use.
7. When proper records of estrual cycles and breeding methods and dates are kept.
8. When no members receive special privileges.
9. When the members realize that only healthy animals can be expected to conceive and that artificial insemination cannot be expected to result in a greater percentage of pregnancies than natural service.

Summary.—This chapter has dealt with the newest and most spectacular phase of animal breeding—artificial insemination. We have

learned that this practice has many advantages, the most important of which are the proving and use of good sires, the creation of large line-bred families, and the curtailment of genital diseases. On the other hand, the practice is new, and much remains to be learned about it. It has certain limitations and is capable of abuse. The various methods of collecting semen have been delineated as well as the techniques of examining semen. Finally, the practical operations in the collection, storage, shipment, and use of the semen in inseminating females has been discussed together with the organization and operation of artificial-insemination associations.

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SECTION III

Mechanisms of Heredity

CHAPTER XII

HISTORY AND PROBLEMS OF GENETICS

Genetics is the science dealing with the similarities and differences exhibited by related organisms. The science of genetics is one of the most recent of man's accomplishments, for it came into being with the rediscovery of the Mendelian principles of inheritance in the year 1900. A long series of events, which might be thought of as extending back to the beginnings of agriculture and the artificial selection of breeding animals following their domestication, preceded its birth. There are, however, three very important and definite milestones that mark the progress of events leading up to genetics. The first was the promulgation of the cell theory by Schleiden and Schwann in the year 1838. Hooke had noticed and discussed the cellular structure of cork in 1665, and, though this in itself led to nothing of moment, it is the historical introduction of the cell theory. The work of Schleiden with plants and Schwann with animals indicated that all living forms were built up of smaller units called *cells*. The discovery of the physical make-up of living things was significant. It founded the science of cytology, which after a rather slow beginning has yielded abundant returns, especially since 1870. The next milestone was that of the establishment of the evolutionary theory.

As we saw in Chap. III, many men had theorized about an evolutionary process before Charles Darwin in the nineteenth century marshaled the evidence that made it seem the most plausible explanation of the presence of the manifold forms of life which have inhabited or do inhabit the planet Earth. Likewise, the work of many men since Darwin's time has added to the plausibility of the theory. This theory ties all living forms into one organic related whole, with the whole of organic life subject to the same basic physiological laws and principles of conception, birth, metabolism, reproduction, inheritance, and death. Evolution postulates that all forms of life have arisen from other preexisting forms back to the time when life had its origin from nonliving materials, and that the rise of new species has been due to variation and selection.

Evolution, therefore, is racial "becoming," whereas genetics is individual "becoming," the same general principles underlying both processes. The third milestone was Mendel's epochal work on the behavior of characteristics in transmission, concerning which the next several chapters will deal.

Content of Genetics.—Bateson in 1906 coined the term *genetics*, which from its derivation from the Greek root *gen*, to become, literally means the *beginning*, or *coming into being*, of organic life. Genetics, however, does not stop with parturition or birth, but rather it expresses the idea of the full becoming of the individuality of the organism. This point should be borne in mind constantly by the student. Broadly speaking, genetics is the study of the why and wherefore of individuality. It is obvious that the individual will be either like its parents or different from them. What genetics attempts to do is to systematize knowledge regarding these similarities and differences and to furnish a rational explanation for them.

There is an old deep-rooted belief to the effect that "like begets like." Experience teaches that sows bring forth pigs not calves, and in this sense "like begets like," but, when the attempt is made to apply the idea in minute details to parent and offspring, difficulties are encountered. Although there may be, and generally is, a greater or less degree of similarity between the two, the expectation that parent and offspring may be exactly alike causes many a disappointment. The fact of the continuity of the germ plasm would lead one to expect that offspring would resemble their parents to a greater or lesser degree, and this, in truth, is just what observation teaches. Any organism receives the determiners for all its potentialities from its ancestors through its immediate parents. It is inconceivable that they could come from any other source, and there is no evidence that any animal can exceed in its accomplishments the upper limit set by its inheritance.

The sum total of all the possibilities and accomplishments of an organism is its individuality. This may appear as the expression of characteristics exactly similar to those exhibited by any of its ancestors, a blend or a mosaic of ancestral characteristics, or one or many very different characteristics due to the interaction of ancestral genes or to mutation. Strictly speaking then, it may be seen that an organism's individuality is the sum total of all its characteristics which result from the union of germ cells produced by its particular parents plus the influence of the environment in which the individual develops. Genetics is the science dealing with individuality, which, in turn, consists of ancestral similarities and differences. The whole matter of inheritance including both similarities and differences is generally spoken of as *heredity*.

Environment and Training.—Two organisms may have different genes but be similar in appearance or behavior because of the environment. Likewise two organisms may have identical genes but be different because of the environment. We shall lay particular stress upon the complement of ancestral determiners, or upon an animal's inheritance. The student, however, must not forget that two other influences aid in shaping individuality, *viz.*, environment and training. Any individuality is a product of the interactions of these three influences and, although resting on the complement of ancestral determiners as its base, this does not in any way minimize the influence of the other two. Many variations are due to environmental causes. The complement of ancestral determiners, however, does set the upper limit that an organism can reach. It is a breeder's province, therefore, to select breeding animals

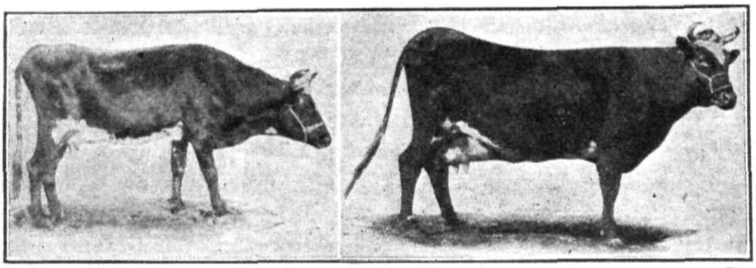

FIG. 71.—A scrub cow before and after being subjected to a good environment. Besides the increase in condition evidenced in the pictures she increased in production 2,814.6 pounds of milk and 113.75 pounds of fat. (*From Iowa Exp. Sta. Bull.* 188.)

that will set a high upper limit for their offspring and then so to modify environment and training that that limit may at least be approximated.

Pre-Mendelian Animal Breeding.—Man has been selecting plants and animals for an unknown period of time, perhaps 10,000, 25,000, or 50,000 years. His method has always been the very simple one of mating what he considered desirable animals and basing his hopes on the general principle that "like begets like." From an early date his selections were probably influenced to some extent by a consideration of pedigree and also to some extent by demonstrated ability to beget desirable offspring. Up until the very recent past, the mechanisms of reproduction, hereditary transmission, and variation were totally unknown. Just by trial and error man made wonderful progress in creating more beautiful and efficient animal types. The scientific basis of inheritance has unfolded rapidly since 1900, so that the modern breeder need no longer be handicapped by a lack of the knowledge of basic principles.

It is sometimes disparagingly remarked that man has made no progress in breeding better livestock for the past 100 years. Since the breeder is

unable, up to the present at least, to create new genes for desirable characters, such a statement is tantamount to saying that breeders have not discarded any undesirable genes or increased the number of desirable ones, or put them together into any new and better combinations. In other words, such a remark means that the proportion of bad genes and good genes is the same in our present-day livestock as it was 100 years ago. Such a statement can be neither proved nor disproved in terms of the actual genes, and, because records of average accomplishment are totally lacking for the old animals and not very numerous for the present ones, and because nutritional and other environmental conditions have undergone such revolutionary changes, the statement can neither be proved nor disproved in terms of records. Crude as may have been our tools of selection, the writer is of the opinion that considerable progress has been made. And he is also of the opinion that the average merit of our animals can now be fairly speedily enhanced, because the basic principles of hereditary transmission are now known.

In the first chapter we sketched briefly the known history of animal breeding. Tablets and monuments from early Egyptian and Babylonian civilizations of 5,000 years ago depict very good types of cattle, sheep, and dogs, and it is known that these peoples used the ass as a beast of burden. The ancient Greek and Roman civilizations also had well-developed arts of agriculture and animal husbandry. During the Middle Ages there were undoubtedly local varieties of animals of good individual merit, but this period is noteworthy from our standpoint mainly as the time when the Arabian horse and the Merino sheep were developed. When Robert Bakewell started farming at Dishley in 1760, the real foundations of our present-day breeds began to be laid, and during the next 100 years practically all the breeds of livestock now found in America were developed. Then, roughly from 1860 to 1900, the breed associations for pedigreeing, protecting, and promoting the various breeds were established, the whole of the above process taking place before the principles underlying reproductive physiology and hereditary transmission were known, although spermatozoa had been discovered by Leeuwenhoek and Ham in 1677 and the ovum by von Baer in 1820. During all this period men had to breed by rule-of-thumb methods, and it is likely that magic and superstition played a large part in breeding operations.

Pre-Mendelian Plant Breeding.[1]—Conditions were very similar in the domain of plant breeding, good varieties of plants having existed and having been continuously improved since the remotest time. A German, Camerarius, discovered the sexual nature of plants in 1694, and in 1717 an Englishman, Fairchild, reported the first artificial plant hybrid.

[1] See Cook, R., A Chronology of Genetics, *U.S. Dept. Agr. Yearbook*, pp. 1457–1477, 1937.

This was followed by extensive work in crossing plants during the next 50 years, climaxed by Kölreuter's work in Germany in the 1760's. During the next 100 years, plant hybridizers discovered and reported the occurrence of dominance, recessiveness, segregation, hybrid vigor, and unit characters, but these isolated facts were not synthesized into a pattern of principles of inheritance, and the statistical relations indicating the uniformity of the behavior of the hereditary units were not recognized. The cell theory was advanced by Schleiden and Schwann in 1838. The decade 1840–1850 saw the beginning of the progeny testing of plants by Vilmorin, the figuring of the chromosomes by Hofmeister, the enunciation of the general principle of the continuity of the germ plasm by Owen, and the observation of actual fertilization of the egg by the sperm in seaweed by Thuret. In 1858, Virchow finally disposed of the old conception of spontaneous generation by means of his pronouncement, *omnia cellula e cellula* (every cell from a cell).

Then within a period of 7 years two of the most famous works of all time came off the press: Darwin's "Origin of Species" in 1859 and a paper by Mendel, "Plant Hybridizations," in 1866. The former created an immediate sensation, the latter, although it contained a clear and concise treatment of the basic principles of inheritance with practically perfect statistical results to buttress them, lay unnoticed for 34 years.

During these years great advances were made in the field of cytology. Hertwig proved in 1875 that fertilization consisted of the union of male and female pronuclei, which established the equal importance of both parents in hereditary transmission of potentialities; Flemming reported the splitting of the chromosomes in 1879; van Beneden the reduction of the number of chromosomes to one-half in the germ cells in 1883; Hertwig, Strasburger, Kölliker, and A. Weismann in 1884–1885 independently and practically simultaneously identified the cell nucleus as the basis of inheritance; and in 1888 the chromosomes were named by Waldeyer.

In the field of the practical, the progeny test in plant breeding was further developed, trap-nesting of poultry begun, and the Babcock test for determining the butterfat percentage of milk discovered. In 1891, Hays proposed the centgener method of progeny testing as the only adequate method for determining the genetic make-up and breeding worth of an individual. Statistical treatment of variation by means of correlation was devised by Galton in 1886, and the standard-deviation technique for determining the significance of deviations from theoretical perfection was developed by Pearson in 1898.

Breeding Advance since 1900.—With the independent rediscovery of the basic principles of inheritance by deVries, Correns, and von Tschermak in 1900 and the bringing to light of Mendel's original work, a new impetus was given to both the scientific and practical aspects of

plant and animal breeding. These principles were demonstrated in animals by Cuenot in 1902 and in man by Davenport in 1904. The interrelations between the behavior of the chromosomes cytologically and the transmission of characters genetically was shown by Sutton in 1903, and the mechanism of sex determination suggested by McClung in 1902 was confirmed by Stevens and Wilson in 1905. The term *genetics* was coined by Bateson in 1906 and the theory of the gene was developed by Morgan and his collaborators at Columbia University in 1910, based upon experiments with the pomace fly, *Drosophila melanogaster*, which has a generation in 10 days numbering up to 400. Following the lead of Shull and East, many inbreeding and crossbreeding experiments were begun both to test and amplify the genetic theory and to try to develop true-breeding strains of both plants and animals. A host of discoveries of chromosome behavior in inheritance have developed since 1910, linkage, crossing over, the nature and production of polyploids, linear order of the genes, interference, limitation of the linkage groups, position effects, the function of inbreeding in reducing heterozygosity, the lethal action of certain genes, etc., the details of which we will meet in later chapters. Finally in 1927 came the artificial induction of mutations by X rays (Muller) and in 1933 the complete unification of cytology and genetics through Painter's work with the giant chromosomes found in the salivary glands of larval Drosophila.

The possibilities inherent in the application of genetic principles to the improvement of both plants and animals have become especially recognized since about 1920. In plants, many new varieties have been made to order and "hybrid corn" is now used extensively throughout the corn belt. In animals we have again centered our attention on the basic fundamentals of proving sires by means of their progeny, as Bakewell did in the eighteenth century and as Varro suggested to Roman farmers in the first century B.C.

Genetics, or the science of breeding, has had a phenomenal development since 1900. The earliest characters studied were the most obvious external ones, such as color, horns, etc. This led some to expect that all animal characters would follow some such simple pattern of inheritance, and as a consequence many unjustifiable claims were made relative to the easy and rapid revolution in breeding practices soon to be achieved by means of genetics. The basic principles of inheritance have been revealed by means of the experimental breeding of small inexpensive and rapidly breeding forms. The detailed mode of inheritance of most of the commercially valuable characters of our larger forms of livestock are still unknown. This is due in large part to the fact that they are probably determined by scores or hundreds of genes and also to the fact that in a normal lifetime of any of the larger mammals we can get so few

offspring. If cows or mares could have several hundred immediate offspring, modes of inheritance of their characters would be much more readily ascertainable. The use of artificial insemination with males of these species should be useful in this regard.

Fortunately, we do not need to wait for the details to be discovered any more than we needed to wait until the exact nature of electricity should become known before putting it to use. Knowledge of the broad basic principles, which we now have, will expedite breeding progress tremendously whenever we develop the ingenuity and desire to really put it to work.

The student should keep in mind during the reading of the next few chapters that the facts revealed by means of breeding experiments furnished the materials on which various portions of the theory of inheritance are based rather than the reverse of this process. Breeding facts supply the materials from which a working hypothesis can be formed. Further experiments are then devised to test the validity of the hypothesis. Such is the *modus operandi* of science.

Problems of Genetics.—The principal problem of genetics is of a threefold nature. Obviously the geneticist is primarily concerned with the mode of transmission of potentialities from parent or other ancestor to offspring. The solution of this problem is of scientific interest, but much more so is it of practical concern. On its solution hinges our ability to create plants and animals of a more useful type, more useful in terms of efficiency, productivity, longevity, as well as those more able to withstand the onslaughts of drouth, disease, and insect pests. With this knowledge, man can, if he wishes, gradually eliminate various sorts of defectives from his own ranks.

In addition there are two other problems facing geneticists. One of these has to do with the physico-chemical nature of the gene itself, which, when solved, may throw considerable light on the origin and development of life in an evolutionary sense. The third problem has to do with the developmental processes of the embryo, the forces and interactions between the genes, the cytoplasm and the environment leading to the organization of the material into a specific pattern.

Problem of Physicochemical Cause.—An elaboration upon the physicochemical entities that probably function in the transmission of similarities or the rise of differences belongs in the fields of chemistry and cytology. Much progress has already been made here, and it is through the cytological behavior of chromosomes that the foundation for present-day genetics has been laid. Research has established the fact that the behavior of the chromosomes in gametogenesis exactly fits the observed appearance and distribution of characters in the developed individual. This is an accomplishment of the greatest moment. There

is no doubt but that the chromosomes constitute the main "bridge of inheritance." The function of the cytoplasm of the cell is not to be overlooked, but it seems to be no more than secondary to the nuclear material

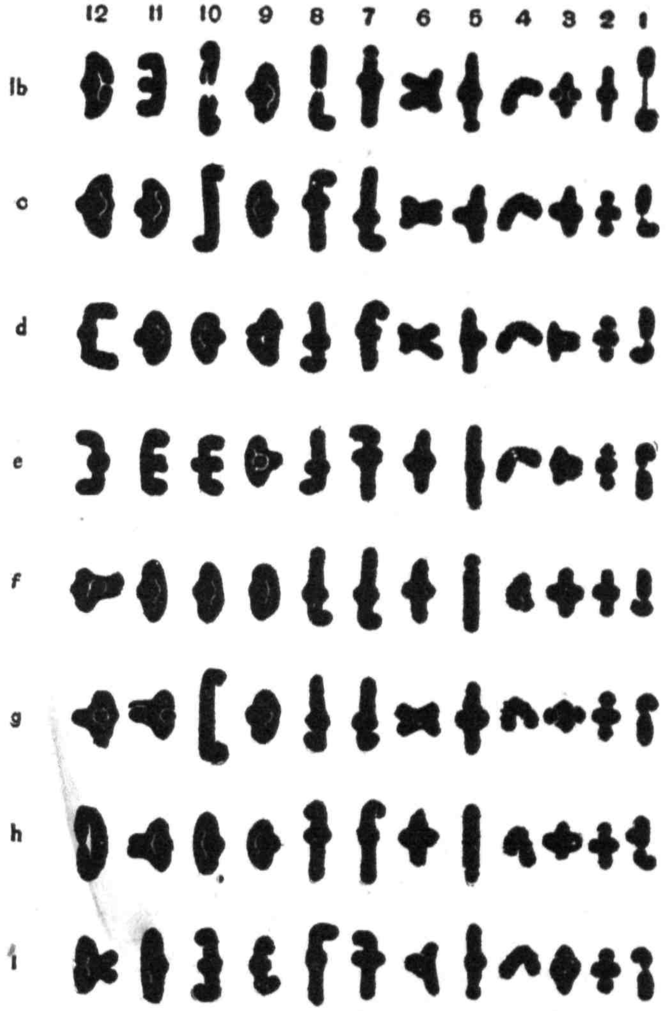

FIG. 72.—Eight chromosome groups of twelve chromosomes each of *Trimerotropis*. (*From Morgan after Carothers, Physical Basis of Heredity, J. B. Lippincott Company.*)

contained in the chromosomes. In the case of certain plants, there is genetic evidence that seems to indicate that certain chlorophyll characteristics of these plants are controlled by plastids which are distributed in a more or less haphazard fashion to the daughter cells, but this is not

a contradiction in any sense of Mendelian inheritance, but only an additional type of inheritance.

Many investigations are now in progress to attempt to learn the nature of the gene and the manner in which it reproduces itself. Nucleic acid has been demonstrated as the characteristic acid of nuclear material. Microchemical analyses have shown that nucleic acid is made up of an inorganic phosphate acid group, a pentose carbohydrate group, together with members of the purine and pyrimidine groups (adenine, guanine, cytosine, thymine, and uracil). It has been shown that the banded regions in the giant salivary-gland chromosomes of larval Drosophila (presumably containing the genes) are much richer in nucleic acid than the clearer spaces between the bands, or disks, and it has been suggested that the ability of a protein to reproduce itself lies in its ability to synthesize nucleic acid. The bands are now thought to be aggregates of nucleic acid arranged across a fibrous protein structure, and the power of the gene to reproduce itself to be due to polymerization and depolymerization brought about in some way by the nuclei acid portion of the molecule. Many investigators now believe that the chromosome is a bundle of protein strands with the genes being the points of attachment to the fibers. The gene is probably a very complex protein, though its definite chemical and physical structure as well as its organization pattern in the chromosome itself are not at present known.

A complete delineation of the chemical make-up of genes and chromosomes may not aid immediately in any practical manner in creating better organisms, but the knowledge for its own sake will be very gratifying when it can be achieved, and future generations may put it to practical use.

Problem of Developmental Organization.—Another great problem is that of hereditary specificity and developmental organization of the individual. In other words, what is the mechanism resident in the fertilized ovum "which impels it to follow in each case a definite line of development"? This problem, unlike that of the nature of the gene and transmission, which deal with the germ plasm, is concerned with the somatoplasm. The method of attack here is the embryological one—not the old descriptive embryology with its manifest limitations in this respect, but the new experimental embryology, "using the term in its widest sense to include the study of such phenomena in regeneration, regulation, growth, etc." This is primarily a study of ontogeny, and it will eventually fill the void now existing between the original zygote with its content of hereditary determiners and the fully developed adult exhibiting the characteristics for which determiners were present in the zygote.

A great deal of intricate experimental embryological research is beginning to shed light on this problem. Transplantation and regenera-

tion techniques have shown that various parts of the body act as organization centers, elaborating hormonallike products which provide the patterns for further development. Belly tissue of the young frog embryo, which, if left in place would have produced skin, will, if transplated early enough to the region of the jaw, produce a normal frog jaw. If, however, it is transplanted to the jaw region of a salamander, it will as formerly produce jaw tissue, but it will be the jaw of a frog because of the frog genes that it contained. Development, therefore, is due primarily to the genes and perhaps secondarily to the interaction of the developing tissues with other nearby tissues, which, of course, have been gene-determined. Also the amputation of half a limb of a salamander will be followed by a complete regeneration of a normal limb, bone as well as muscle and nerves, which indicates a substance in the cells of the

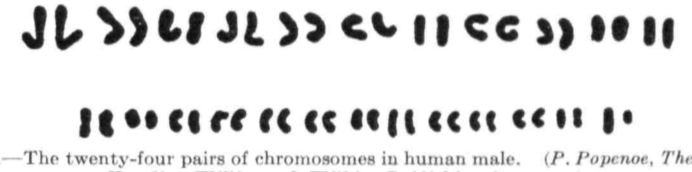

FIG. 73.—The twenty-four pairs of chromosomes in human male. (*P. Popenoe, The Child's Heredity, Williams & Wilkins Publishing Company.*)

stump capable of directing the normal development of the tissues that spring from it.

Problem of Mode of Transmission.—There are two methods of studying the manner in which characteristics are transmitted from one generation to the next. They are (1) by studying the ancestors of certain individuals or (2) by studying the progeny of certain individuals. The former, or ancestor study, may be carried on by means of biometry or by means of data recorded in purebred herd books. The progeny study is the experimental or Mendelian method, in which the matings are planned, and the study may have a statistical basis. Inquiry will now be made into these methods of genetic research, bearing in mind that in this field, particularly, environmental conditions must be carefully controlled so that the observed results may justifiably be attributed to the make-up of the germ plasm.

The statistical method of attacking the problem was originated by Sir Francis Galton, later developed by Karl Pearson, and is known today as *biometry*.

It is a most useful tool in the hands of the analytical geneticist. Its function is to measure the degree of resemblance between related individuals and to express the result in numbers. As pointed out by Pearl, this weakness of the method as a means of research lies in two facts: (1) it is largely a method of description and does not attempt to give the cause of the events, and (2) because biometry gives the degree of resem-

blance between parent and offspring, and because heredity is a cause of the resemblance, the biometrical method (correlation) measures the degree or intensity of inheritance. As Pearl points out, heredity is not the sole cause that can lead statistically to a significant correlation between parent and offspring. "Anything whatsoever which tends to bring about local group differentiation within the sample included in the table will tend to produce the same result, altogether independent of any genetic relationship or the absence of it."

With its limitations and dangers kept in mind, biometry, properly used, is a valuable agent in the study of genetics.

Herd books and production records of livestock may be made to yield valuable information on the problem of hereditary transmission. With the aid of such records, the manner of transmission of superficial characters, such as color markings, set of ears, and so on, as well as the deeper lying functional activities, such as speed, milk production, etc., may be investigated. This method can be criticized as being descriptive rather than experimental, and in it there is also the danger that an investigator may not have access to all the relevant facts. These records are now beginning to yield information that should prove of great value to practical breeders by explaining how certain traits are inherited and possibly also by showing the falsity of timeworn beliefs.

The two preceding methods have dealt with the ancestors. The following will be concerned with progeny. This is the experimental-breeding or pedigree-culture method, which Mendel used so successfully. He succeeded in discovering the basic plan of hereditary transmission, because he reduced his problem to its simplest form and studied one pair of contrasted characters at a time. Like the Galtonian, this method is also statistical. In general, it consists of producing pure races, crossing them, mating the hybrids, and ascertaining the ratios in the F_2 and later generations. This method has also resulted in the establishment of Johannsen's pure-line theory and deVries's mutation theory. The former of these has been defined as "all the progeny of a single self-fertilized individual." Such individuals eventually give rise to inbred strains that are homozygous genetically but with fluctuating variations in each inbred line. These variations are probably due largely to environmental conditions and not to germinal variations. In other words, this points to the static character of the germ plasm, or its conservative nature.

The mutation theory suggested by deVries, on the other hand, postulates sudden heritable changes in the genes. This provides one means of heritable variation and points to the dynamic character of the germ plasm, or its progressive nature.

Finally the organism itself will often provide a partial index to its genetic make-up. If a character behaves as a recessive, we know the

genetic make-up of an animal evidencing this character (for this character). This is true also in a case where dominance is lacking, for the homozygous dominant (AA), the heterozygote (Aa), and the homozygous recessive (aa) will all evidence different expressions of the character. If the character shows complete dominance, however, we will be unable to distinguish between AA and Aa individuals.

In animal breeding, our aim is the creation of desirable and efficient animals that will of necessity transmit their own desirable qualities to a high percentage of their offspring. We want all the evidence that we can get regarding the likelihood that our desirable animals will be good transmitters. Summarizing the above discussion we can get this information from

the individual itself
↙ ↘
its progeny its ancestors

Genetics and the Practice of Breeding.—The practice of breeding is older than history. Its method is selection, and its accomplishments legion. It has produced fast, fancy, and farm horses; increased the yield of milk from a few hundred to 41,000 lb. annually; and has produced the food that has enabled man literally to conquer his world. Genetics acknowledges gladly the achievements of empiricism and seeks the reason "why." The method of practical breeders has always been that of trial and error, and of necessity there has always been a goodly share of the latter. The greatest service that genetics can render to the practice of breeding lies in its ability to analyze and to provide logical explanations. This will inevitably result in the sifting of the true from the false, a service of no mean value and one which is being fulfilled rapidly. If genetics did no more than unearth the principles underlying breeding and post "no-passing" signs at the head of all the blind alleys, it would expedite successful breeding to a marked degree.

However, knowledge gained through genetic studies has already provided new methods that will lead more quickly and surely toward the goal of more beautiful form and more efficient function. Detailed knowledge of the mode of inheritance of most of the characteristics exhibited by higher animals is still unknown and from the very nature of the problem is difficult, though genetics bids fair to furnish the solution. When this has come about and the principles are thoroughly understood, genetics will have proved itself merely the handmaid of animal breeding, to which it will have rendered a valuable service in successfully and firmly fitting into place the keystone of all breeding operations, "rational selection."

To be successful in breeding better livestock, a person should first of all love to work with animals. Next comes the necessity for a thorough

knowledge of the history, accomplishments, and shortcomings of one's particular breed. Practice in livestock judging bulwarked by a knowledge of anatomy and physiology and by experience gained through study of finished carcasses in meats courses should also prove to be very useful. Finally, courses in veterinary hygiene and science, together with the materials presented in the books dealing with animal breeding, should complete one's initial training for animal-breeding work with actual experience in the field serving as a continuing source of enlightenment and inspiration.

Summary.—This chapter serves as a general introduction for our consideration of genetics, which, as we have seen, is concerned with similarities and differences exhibited by related organisms. We have laid particular emphasis on the chromosomes as "the bridge of inheritance," but we should be careful not to overlook the large part played by both environment and training in bringing any inherited character to its full fruition. We traced very hurriedly the long history of both plant and animal breeding and saw how the occasionally observed facts of inheritance down through the ages were finally fitted together into a complete and complex whole by Mendel and his successors. The three principal types of problems that genetics and related sciences are trying to solve were indicated as well as a preview of the methods now being used to effect solutions. Finally, we listed practical prerequisites for the scientific animal breeder and indicated the role of genetics in the practical field of animal husbandry.

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CHAPTER XIII

THE PRINCIPLES OF HEREDITY

Men have been breeding plants and animals for many thousands of years. In the earliest stages of breeding, the main purpose was probably that of seizing upon favorable variations in order to try to improve both plant and animal species. By allowing these favorable variates to have many offspring and less desirable ones to have few or none, a slow, steady improvement ensued. The question was, "how" can we secure better plants and animals to serve our human needs?

Early man, like children of today, was probably randomly curious. He wondered in a vague way about the stars, his own whence and whither, etc. The early Egyptians and, later, the Greeks began to develop a system of experimental observation and inquiry, but later events put a stop to these beginnings. Up until about the year 1500, authoritarianism (believing what others had said) and the fear of religious persecution succeeded in quite thoroughly throttling any intelligent curiosity. Gradually these shackles were unloosed, and man began to add experimentation to speculation. This was the beginning of the age of enlightenment. Copernicus, Brahe, Kepler, and Galileo soon proved through mathematical calculations and observation that the earth, far from being the center of the universe, was in fact but one of several relatively tiny specks which revolved around a rather puny star, our sun. Newton soon combined the mathematical physics of Descartes and Galileo's law of falling bodies into the gravitational theory of an orderly and immense universe in which nothing is left to chance or caprice.

These discoveries, deductions, and syntheses finally proved that old authorities were not infallible, that observation and common sense had their limitations, because things were not always what they seemed to be and, most important of all, man's own reason backed by observation, calculation, and experiment was the most trustworthy guide available.

Eventually this intellectual curiosity was directed toward the world of living things. Man began to experiment to try to find out "why" the results of certain matings yielded certain results. This was especially true in the plant kingdom, in which many men carried on plant hybridization experiments in attempts to fathom nature's secrets in the transmission of characters from parent to offspring. In 1694, Camerarius published a work which showed that plants were sexual organisms. In 1717 occurred the production of the first artificial plant hybrid by

Thomas Fairchild. The work of Spallanzani in the eighteenth and Pasteur in the nineteenth century proved the old idea of spontaneous generation to be a fallacy; Schleiden and Schwann discovered the cellular nature of plants and animals; and Darwin established the validity of the process of organic evolution.

Finally, breeding experiments with peas carried on from 1857 to 1865 by an Austrian monk, Johann Gregor Mendel, revealed some of the basic principles of hereditary transmission. There had been many other plant hybridizers before Mendel, but he was the first to attack the problem on a large enough scale and in such a thoroughgoing way that it became

FIG. 74.—Gregor Mendel, the discoverer of the laws underlying inheritance.

possible (1) to determine the number of different forms under which the offspring of hybrids appeared, (2) to arrange these forms with certainty according to their separate generations, and (3) to ascertain definitely their statistical relations. In 1866, he published a report of 8 years' hybridization experiments, though 34 years elapsed before the validity of his pioneer work was established. Mendel, like many other men who have thought ahead of their time, died before the results of his splendid pioneering were appreciated.

Like many other natural phenomena, this matter of inheritance yielded to a fairly simple interpretation, and Mendel's success was due in large measure to the fact that he reduced his problem to its very simplest form by studying one pair of contrasted characters at a time, coupled with the fact that he happened to work with characters which were determined by

genes carried in different chromosomes and which therefore assorted independently. Mendel's discovery was duplicated in 1900 by three botanists, DeVries, Correns, and von Tschermak, and this led eventually to the discovery of Mendel's original paper.

Mendel's work laid the basis for the later establishment of two of the general laws of inheritance, *viz.*, those of segregation and of independent assortment. To these have been added, since 1900, the following: linkage, crossing over, linear order, interference, and limitation of the linkage groups. Some of these later principles are in a sense antithetical to the original Mendelian principle of independent assortment, but for the sake of clarity and unity all the phenomena of inheritance, based on the reactions of genes, are generally known under the collective term *Mendelism.*

MENDELIAN TERMS

The following are some of the terms now in general use in referring to Mendelian phenomena.

Unit Characters. Any characters of any organism that behave as a unit in inheritance—plant size in peas, horns in cattle, etc.

Genes. The units of inheritance that probably react together and with the cytoplasm, and these two with the environment to make patent the organism's latent potentialities.

*Allele**. Mendelian characters are inherited in alternative pairs (or series). These alternative forms of a gene, which are located at the same point on each one of a pair of chromosomes, are called *alleles, e.g.*, albinism (recessive), normal pigmentation (dominant); horns (recessive), hornlessness (dominant). (Allelomorph, allelic, adjective—variants.)

*Dominant**. A character, possessed by one of the parents of a hybrid, which is manifested in the hybrid to the apparent exclusion of the contrasted character from the other parent (the recessive). Thus in a cross of green- and yellow-seeded peas the first generation has yellow seeds. Yellow is dominant and green is recessive, being transmitted but not appearing in the presence of the factor for yellow.

Hybrid. The individual that arises from crossing parents which are pure for certain different characteristics. Crossing tall (*TT*) on dwarf (*tt*) peas produces a hybrid (*Tt*).

Monohybrid. A hybrid that is heterozygous for one pair of allelic genes.

Dihybrid. A hybrid that is heterozygous for two pairs of allelic genes.

Trihybrid. A hybrid that is heterozygous for three pairs of allelic genes.

* Definitions marked with an asterisk taken from "Glossary of Genetic Terms," *U.S. Dept. Agr. Yearbook*, pp. 153–164, 1936.

Phenotype. The expressed character (or sum of all the characters) of an organism; *e.g.*, if, in peas, genes for both the tall and the dwarf characteristics (T and t) are present, the pea grows tall, and therefore belongs to the tall phenotype.

Genotype. What an organism actually is as determined by its germ plasm; *e.g.*, TT and Tt are both tall peas, therefore, the same phenotype, but because of their different genotypic constitutions will transmit differently and therefore belong to different genotypes.

*Heterozygote**. An organism to which its two parents have contributed unlike genes with respect to any given allelic pair governing contrasted characters, and which in turn produces two kinds of germ cells with respect to the character. (Heterozygous, adjective.)

*Homozygote**. An organism whose parents contributed to it a similar member of any given pair of genes, and whose germ cells are therefore all alike with respect to the genes for that character. (Homozygous, adjective.)

*Race**. A group of individuals having certain characteristics in common because of common ancestry—generally a subdivision of a species.

Gamete. A reproductive cell of either sex; a sperm or ovum.

*Heredity**. The resemblance, derived from the ancestry, among organisms related by descent.

P. Parental generation.

F_1. First hybrid generation—made by crossing $P \times P$.

F_2. Second hybrid generation—made by crossing two F_1 hybrids.

*Variation**. In biology, the occurrence of differences among the individuals of the same species or variety.

Haploid. Single; referring to the reduced number of chromosomes in the mature germ cells of unisexual organisms (n).

*Diploid**. Having two sets of chromosomes. Body tissues of higher plants and animals are ordinarily diploid in chromosome constitution ($2n$).

*Polyploid**. Normal body cells of the higher plants and animals have two sets of chromosomes. Polyploids are forms having three or more of these basic chromosome sets (3 or more n).

*Heteroploid**. An organism characterized by a chromosome number that is not a multiple of the basic haploid number.

The Essence of Mendelism.—One of Mendel's experiments involved the crossing of tall and dwarf peas, and he found that all the offspring grew tall, because in this species tall growth is dominant over dwarf. When these F_1 hybrids were crossed, the resulting F_2 generation consisted of tall peas and dwarf peas in the ratio of 3:1. The following diagram should make this clear:

TT — pure tall parent — *T* — pollen after reduction

tt — pure dwarf parent — *t* — ovules after reduction

Tt F_1 hybrid (tall) {either ovule fertilized by either pollen}

T *t* pollen of hybrid after reduction

T *t* ovules of hybrid after reduction

TT *Tt* *Tt* *tt*

tall : dwarf

3 1

The *TT* peas are pure for tallness and will produce all tall offspring. The same holds true for the *tt* peas in respect to dwarfness. The two *Tt* peas are phenotypically tall, but carry the factor for dwarfness *t* as a recessive. Two of these crossed would again give:

T *t*

T *t*

TT, *Tt*, *Tt*, *tt*, etc., ad infinitum

This 3:1 ratio is phenotypic, the genotypic ratio being 1:2:1. This was the gist of Mendel's work; *viz.*, starting with parents pure for some contrasted character, hybrids would be produced in the F_1 that looked like the dominant parent; and, in the F_2, ¼ of the population would be pure for one grandparental characteristic, ¼ pure for the other grandparental characteristic, and ½ would carry both factors and resemble the dominant parent.

Mendel's Hybridization Experiments.—It is of importance to know how far Mendel's results and later experiments meet mathematical expectations. For this reason it will be well to consider both Mendel's original work and some later experiments. The point at issue is whether Mendel discovered an interesting restricted phenomenon in peas or a universal law of inheritance.

Mendel secured some 34 more or less distinct varieties of peas and, before beginning his own experiments, subjected them to a 2-year trial to ascertain whether or not they would breed true to type. Knowing that some characters of plants are transmitted unchanged to the hybrids and their progeny and that one of each pair of contrasting characters of two plants appeared in the hybrid as the dominant character, whereas the other (recessive) reappeared in the progeny of the hybrid, Mendel planned his experiment to observe and record the proportion of each

pair of differentiating characters in the succeeding generations of hybrids and to deduce the law according to which they appear in the successive generations.

Mendel selected the following seven pairs of contrasted characters for study:

1. The difference in the form of the ripe seeds. These are either round or roundish,[1] the depressions, if any, occur on the surface, being always only shallow; or they are irregularly angular and deeply wrinkled.

2. The difference in the colour of the cotyledons. The albumen of the ripe seeds is either pale yellow, bright yellow, and orange coloured, or it possesses a more or less intense green tint.

3. The difference in the colour of the seed coat. This is either white, with which character white flowers are constantly correlated; or it is grey, grey brown, leather brown, with or without violet spotting, in which case the colour of the standards is violet, that of the wings purple, and the stem of the axils of the leaves is of a reddish tint. The grey seed coats become dark brown in boiling water.

4. The difference in the form of the ripe pods. These are either simply inflated, not contracted in places; or they are deeply constricted between the seeds and more or less wrinkled.

5. The difference in the colour of the unripe pods. They are either light to dark green or vividly yellow, in which colouring the stalks, leaf veins and calyx participate.

6. The difference in the position of the flowers. They are either axial, that is, distributed along the main stem; or they are terminal, that is, bunched at the top of the stem and arranged almost in a false umbel; in this case the upper part of the stem is more or less widened in section.

7. The difference in the length of the stem. The length of the stem is very various in some forms; it is, however, a constant character for each, in so far that healthy plants, grown in the same soil, are only subject to unimportant variations in this character.

In experiments with this character, in order to be able to discriminate with certainty, the long axis of 6 to 7 feet is always crossed with the short one of ¾ to 1½ feet.[2]

The results of segregation in the F_2 in those seven series of experiments by Mendel are shown in Table 17.

Mendel was dealing with strictly contrasting characters and got no intermediate or blending forms. The matter of personal bias was therefore obviated. The phenotypic ratio that Mendel secured in the F_2 with each pair of contrasted characters was in no case significantly

[1] In each case the dominant character is underscored.

[2] CASTLE, W. E., "Genetics and Eugenics," p. 317, Harvard University Press, Cambridge, Mass., 1916.

different from 3:1. Many other investigations of single contrasting characters have yielded a similar 3:1 phenotypic ratio in the F_2.

Mendel carried some of the descendants of the above hybrids along through four to seven generations and reported that "no departure from the rule has been perceptible."

TABLE 17.—SUMMARY OF MENDEL'S EXPERIMENTS WITH PEAS

Number	Character contrast	Number in F_2	Dominants	Recessives	Ratio
1	Form of seed	7,324	5,474	1,850	2.96:1.00
2	Color of cotyledons	8,023	6,022	2,001	3.01:1.00
3	Color of seed coats	929	705	224	3.15:1.00
4	Form of pod	1,181	882	299	2.95:1.00
5	Color of pod	580	428	152	2.82:1.00
6	Position of flowers	858	651	207	3.14:1.00
7	Length of stem	1,064	787	277	2.84:1.00
Totals		19,959	14,949	5,010	2.99:1.00

He also made crosses of individuals differing simultaneously in two and in three characteristics and found the same underlying principle active; *viz.*, the F_1 hybrids looked like the sum of the dominant characters put in by both parents, and in the F_2 all the characteristics were recombined into all the possible combinations.

The Mendelian Theory of Inheritance.—The essence of Mendel's work is summed up in this statement of Mendel's.

The results of the previously described experiments led to further experiments, the results of which appear fitted to afford some conclusions as regards the composition of the egg and pollen cells of hybrids. An important clue is afforded in Pisum by the circumstance that among the progeny of the hybrids constant forms appear, and that this occurs, too, in respect of all combinations of the associated characters. So far as experience goes, we find it in every case confirmed that constant progeny can only be formed when the egg cells and the fertilizing pollen are of like character, so that both are provided with the material for creating quite similar individuals, as is the case with the normal fertilization of pure species. We must, therefore, regard it as certain that exactly similar factors must be at work also in the production of the constant forms in the hybrid plants. Since the various constant forms are produced in one plant, or even in one flower of a plant, the conclusion appears logical that in the ovaries of the hybrids there are formed as many sorts of egg cells, and in the anthers as many sorts of pollen cells as there are possible constant combination forms, and that these egg and pollen cells agree in their internal composition with those of the separate forms.

In point of fact, it is possible to demonstrate theoretically that this hypothesis would fully suffice to account for the development of the hybrids in the separate

generations, if we might at the same time assume that the various kinds of egg and pollen cells were formed in the hybrids on the average in equal numbers.[1]

Mendel's results were published in 1866, and his paper was discovered by deVries, a Dutch botanist, in running down the literature on plant hybridization following his own experiments with the evening primrose, from which work he formulated his theory of mutations and his law of "the splitting of hybrids." Apparently Correns in Germany and von Tschermak in Austria discovered the latter principle at about the same time.

The principles evidenced by the work of Mendel, deVries, Correns, and von Tschermak have since been named *segregation* and *independent assortment*.

1. *Segregation.* A new individual arises from the union of a male and a female gamete that contain a sample half of the complete genetic material of each parent, *i.e.*, one or the other member of each pair of chromosomes. Each parent contributes a complete haploid set of chromosomes to each of its offspring. When this new individual matures and begins to produce germ cells, the latter go through the process of reduction, at which time the chromosomes put in by the parents segregate or separate out from each other, one member of each pair going to each of the secondary germ cells, in all the possible combinations. This principle is illustrated in the tall- and dwarf-pea cross, the pollen or ovules produced in the F_1 hybrid containing a chromosome in which is located either the gene for tallness or the gene for dwarfness.

2. *Independent Assortment.* The chromosomes of the hybrid assort themselves at reduction into all possible combinations, each germ cell necessarily having one member of each pair of chromosomes. With one pair of chromosomes, two genetically different germ cells are produced (2^1); with two pairs of chromosomes, four genetically different germ cells are produced (2^2); with three pairs, eight genetically different germ cells are produced (2^3); etc. Chromosomes and genes were unknown in Mendel's day. He did not speak of them but rather in terms of the characters of his plants. Since, however, all of the characters in peas with which Mendel worked were apparently determined by factors (genes) located in different chromosome pairs and no two of them by genes in the same pair of chromosomes, Mendel was able to postulate the most important principle of inheritance, independent assortment, which actually applies to chromosomes and not, as Mendel perhaps thought, to characters.

Segregation and independent assortment constitute two of the basic principles of inheritance. For independent assortment or distribution of characters, the pairs of contrasting characters considered must be deter-

[1] *Ibid.*, p. 332.

mined by genes carried in different chromosomes. If the two or more pairs of contrasted characters were determined by genes carried in the same chromosome, they would not be expected to assort independently but rather to remain linked together. Linkage relations will be discussed later.

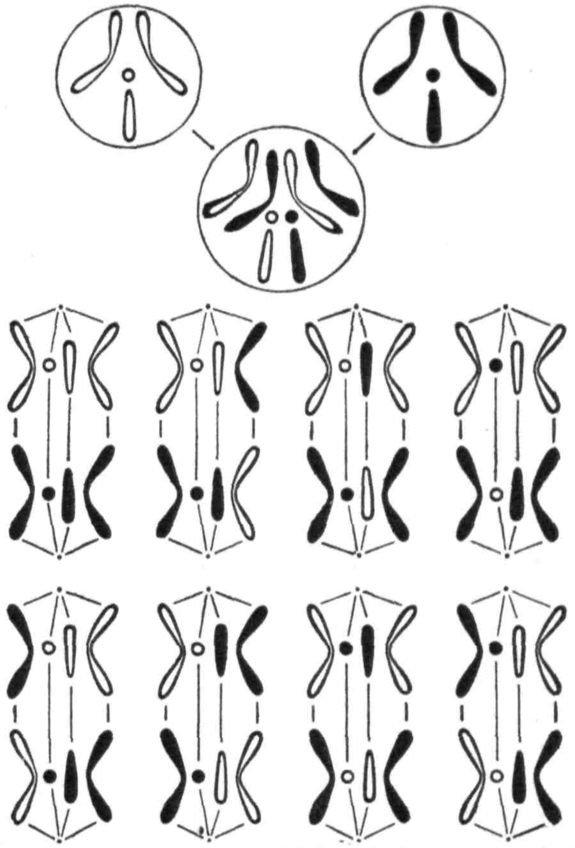

FIG. 75.—Diagram showing consequences of independent segregation of chromosomes in *Drosophila ampelophila*. (*From Babcock and Clausen, Genetics in Relation to Agriculture.*)

Monohybrid Crosses.—A monohybrid is a hybrid that is heterozygous for one pair of allelic genes. When we cross a homozygous tall parent (*TT*) with a homozygous dwarf (*tt*) we get a monohybrid (*Tt*). If two of these monohybrids are crossed, we get a ratio of 3 tall:1 dwarf offspring. For an explanation of these breeding facts we assume that one parent has the genes for tall growth and the other parent the genes for dwarf growth at similar loci in homologous chromosomes, and that these genes are both present in the monohybrid but separate or segregate

Experience has shown that the polled condition is dominant over the horned condition, and black color over red in cattle.

The genes for polled or horned and for black or red are apparently located in different chromosomes, because, when we mate dihybrids *Pp Bb*, we get a ratio of

9 polled blacks
3 polled reds
3 horned blacks
1 horned red.

indicating that the germ cells containing genes *PB*, *Pb*, *pB*, and *pb* were produced in equal numbers by all these dihybrids.

The nine polled black individuals are of the same phenotype but the nine are made up of

1 *PP BB*
2 *PP Bb*
2 *Pp BB*
4 *Pp Bb*

or four different genotypes in the same phenotype, and the only way to ascertain the different members of these four genotypes is through breeding trials. This brings to our attention a very important practical consideration, *viz.*, that we can't always tell by the appearance or performance of an animal, its phenotype, how it will transmit. The *PP BB* animal is polled and black and all of its offspring will be polled and black, because it must transmit both gene *P* and gene *B* to all its get. But the *Pp Bb* animals are also polled and black, but these animals may transmit the combinations of *PB*, *Pb*, *pB*, or *pb* genes to their offspring. One of the latter animals (*Pp Bb*) if mated to horned, red animals will get offspring as indicated below;

	PB	*Pb*	*pB*	*pb*
pb	*Pp Bb* polled, black	*Pp bb* polled, red	*pp Bb* horned, black	*pp bb* horned, red

whereas a homozygous polled, black animal, *PP BB* (germ cells all *PB*), if mated to horned, red animals will get all polled, black offspring, *Pp Bb*. The way in which an animal will transmit depends on its genotype, which may or may not correspond with its phenotype. The later chapters of this book on selection in horses, cattle, sheep, and swine will be devoted quite largely to a consideration of the procedures necessary to learn the genotypic make-up of our breeding animals.

A situation similar to the two dihybrid examples described above prevails in the inheritance of comb shape in poultry, but here the two pairs of factors influence only *one* characteristic instead of two. In this case

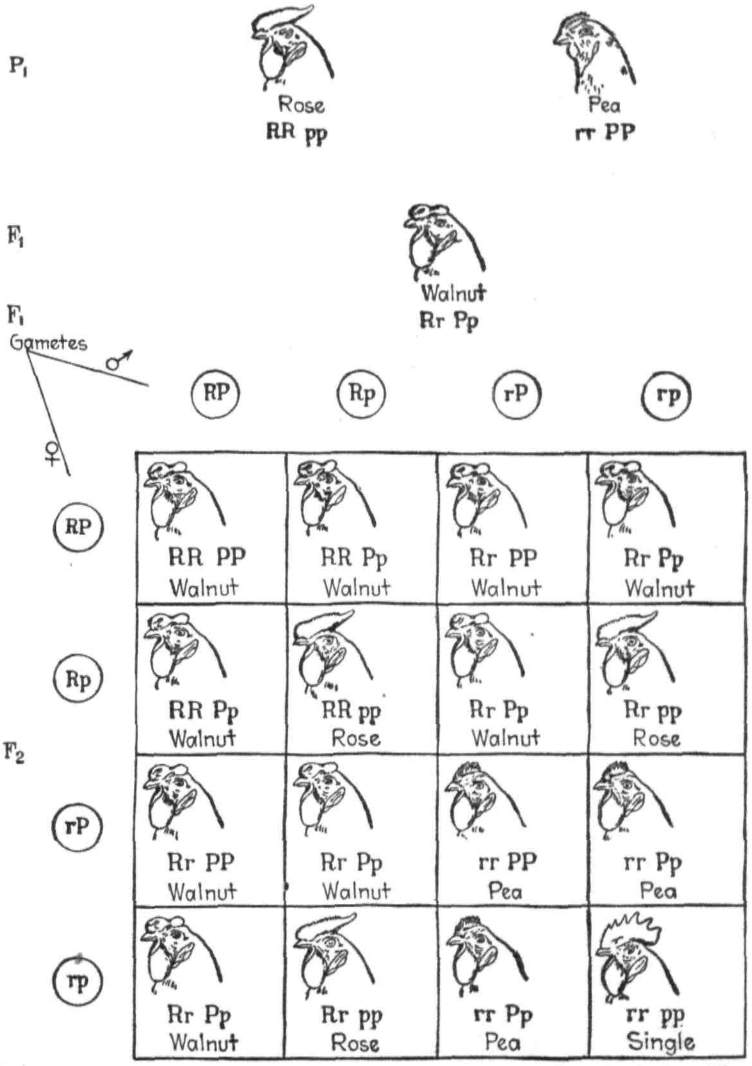

FIG. 77.—Diagram showing interaction of factors for comb form in fowls. The cross of a pure rose-comb bird with a pure pea-comb one gives all walnut-combed offspring. The 16 possible combinations of the F_1 gametes, with their genotypes and the phenotypes resulting from factor interaction, are shown in the F_2 checkerboard. (*From Sinnott and Dunn.*)

RR pp birds are rose-combed, *rr PP* birds are pea-combed, and, when these are crossed, giving *Rr Pp*, the combs are walnut-shaped. Crossing two walnuts, *Rr Pp*, gives 9 walnuts, 3 rose, 3 pea and 1 single comb, *rr pp*.

Trihybrid Crosses.—A trihybrid is one that is heterozygous for three pairs of allelic genes. The reader can now figure out for himself the results to be expected from crossing the trihybrids secured from mating a

rough, black, short-haired guinea pig = *RR BB SS*.

to a

smooth, white, long-haired guinea pig = *rr bb ss*
giving the trihybrid rough, black, short *Rr Bb Ss*

remembering that these trihybrids can secrete the following sorts of germ cells (for these genes are in different chromosomes): *RBS*, *RBs*, *RbS*, *Rbs*, *rBS*, *rBs*, *rbS*, *rbs*.

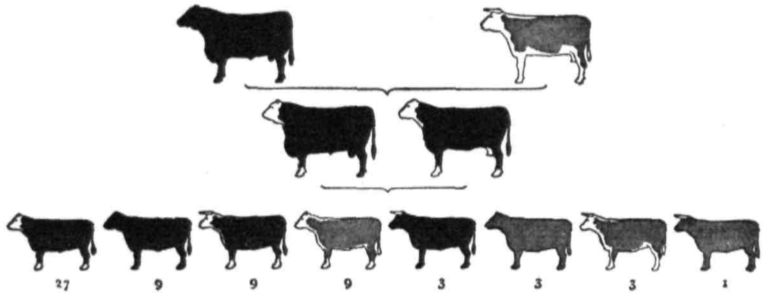

FIG. 78.—Diagram showing inheritance of polled, white face, and black body characteristics and their allelomorphs in an Angus-Hereford cross through F_2.

A similar problem can be worked out in cattle involving the crossing of Angus and Herefords.

Angus (polled,[1] black body, black face) = *PP BB ww*
Hereford (horned, red body, white face) = *pp bb WW*

The monohybrid cross = 3:1 ratio
The dihybrid cross = $(3:1)^2$ ratio, or 9:3:3:1
The trihybrid cross = $(3:1)^3$ ratio, or 27:9:9:9:3:3:3:1

Multifactor Crosses.—Little and Phillips report an experiment involving four pairs of independently Mendelizing factors in mice. They

[1] In crosses between polled and horned breeds of cattle the offspring are not by any means all polled, even though it is true that the latter condition is due to a dominant gene and in spite of the fact that the polled parent is homozygous. Some scurred and horned animals usually appear. This can be explained by postulating a gene for scurs (*Sc*), which is epistatic to polled (*P*) in either heterozygous (*Sc sc*) or homozygous (*Sc Sc*) males, but which is epistatic only in females that are homozygous (*Sc Sc*). A similar epistatic relation apparently holds for a special horn gene (*Ha*), distinct from the gene (*H*), carried by all horned breeds, and found principally in certain horned breeds of Africa. (*Kans. Agr. Expt. Sta. Rept.* p. 87, 1936.)

crossed a wild male of the genetic constitution *AA BB DD PP* (*A* for agouti pattern, *B* for black coat, *D* an intensity factor, and *P* a factor for eye coloration) on a pink-eyed, dilute, brown female of the genetic constitution *aa bb dd pp*. The observed ratios from such a cross in the F_2 were in all cases very close to expectations. The chromosomal interpretation of the segregation and recombination of factors in this cross is the same as was found in the mono-, di-, and trihybrids.

In the case of a monohybrid, 4 individuals are secured in the F_2 checkerboard; a dihybrid gives 16; a trihybrid 64. One involving four pairs of contrasted characters would furnish 256 individuals in the F_2; and, if ten characters were considered simultaneously, 1,048,576 individuals would have to be considered in the F_2 generation. It can readily be seen that the problem is becoming unwieldy. For this reason, very few crosses involving as many as four pairs of contrasted characters have been worked out.

Most of the commercially important characters of our farm mammals do not behave in inheritance as though they were determined by only one, two, or three pairs of genes, but rather as though they were determined by the combined interaction of dozens or scores of pairs of genes, probably scattered through all the chromosomes. A different technique must, therefore, be employed when dealing with characters determined by many genes. Even though a character was determined by as few as three genes, we have seen that in the F_2 we could get eight different genotypes.

27 with at least one *A*, one *B*, and one *C*.
9 with at least one *A*, one *B*, and *c*'s.
9 with at least one *A*, *b*'s, and one *C*.
9 with *a*'s, one* *B*, and one* *C*.
3 with at least one *A*, one *B*, and *c*'s.
3 with *a*'s, one* *B*, and *c*'s.
3 with *a*'s, *b*'s, and one* *C*.
1 with *a*'s, *b*'s, and *c*'s.

* At least.

Ova	Spermatozoa: *PWB*	*PWb*	*PwB*	*Pwb*	*pWB*	*pWb*	*pwB*	*pwb*
PWB	*PP WW BB*	*PP WW Bb*	*PP Ww BB*	*PP Ww Bb*	*Pp WW BB*	*Pp WW Bb*	*Pp Ww BB*	*Pp Ww Bb*
PWb	*PP WW Bb*	*PP WW bb*	*PP Ww Bb*	*PP Ww bb*	*Pp WW Bb*	*Pp WW bb*	*Pp Ww Bb*	*Pp Ww bb*
PwB	*PP Ww BB*	*PP Ww Bb*	*PP ww BB*	*PP ww Bb*	*Pp Ww BB*	*Pp Ww Bb*	*Pp ww BB*	*Pp ww Bb*
Pwb	*PP Ww Bb*	*PP Ww bb*	*PP ww Bb*	*PP ww bb*	*Pp Ww Bb*	*Pp Ww bb*	*Pp ww Bb*	*Pp ww bb*
pWB	*Pp WW BB*	*Pp WW Bb*	*Pp Ww BB*	*Pp Ww Bb*	*pp WW BB*	*pp WW Bb*	*pp Ww BB*	*pp Ww Bb*
pWb	*Pp WW Bb*	*Pp WW bb*	*Pp Ww Bb*	*Pp Ww bb*	*pp WW Bb*	*pp WW bb*	*pp Ww Bb*	*pp Ww bb*
pwB	*Pp Ww BB*	*Pp Ww Bb*	*Pp ww BB*	*Pp ww Bb*	*pp Ww BB*	*pp Ww Bb*	*pp ww BB*	*pp ww Bb*
pwb	*Pp Ww Bb*	*Pp Ww bb*	*Pp ww Bb*	*Pp ww bb*	*pp Ww Bb*	*pp Ww bb*	*pp ww Bb*	*pp ww bb*

FIG. 79.—Checkerboard of F_2 cross between a polled, black-faced, black-bodied Angus and a horned, white-faced, red-bodied Hereford.

This is a total of 64 individuals in the F_2 and represents 27 different genotypes. Only one of these genotypes (the last one, involving all small letters, can be recognized on sight, so that breeding tests would have to be instituted to reveal the genotypic differences between *AA BB CC* and *Aa BB Cc* individuals, etc. So the fact that there apparently are so few unit characters (determined by one or a few pairs of genes only) in our farm animals is no great loss or hardship, for it is not practical to deal with more than one or two pairs of genes at a time, especially in species which have relatively as few offspring as our farm animals and where the proper combinations of several genes might by chance never be secured in the small numbers available.

The following table should help to make this point clear.

TABLE 18.—RELATION BETWEEN THE NUMBER OF GENE PAIRS INVOLVED IN A CROSS AND THE NUMBER OF PHENOTYPIC AND GENOTYPIC CLASSES IN THE F_2

Number of gene pairs involved	Number of visibly different F_2 classes if dominance is complete	Number of different kinds of gametes formed by F_1	Number of genotypically different combinations	Number of possible combinations of F_1 gametes
1	2	2	3	4
2	4	4	9	16
3	8	8	27	64
4	16	16	81	256
n	2^n	2^n	3^n	4^n

It must be remembered that, in order to secure independent segregation in all the types of hybrids studied above, it is necessary that the genes be located in different chromosomes. This of necessity limits, in any species, the number of pairs of contrasted characters that can show independent assortment to the number of pairs of chromosomes found in that species. *Drosophila melanogaster*, for example, with four pairs of chromosomes could not manifest more than four pairs of independently segregating characters at any one time. No cases have been discovered where there are more independently segregating pairs of contrasted characters than there are pairs of chromosomes. If, in Drosophila, five pairs of contrasted characters were considered at one time, it would, of necessity, mean that at least two of these pairs of characters were determined by factors carried in the same chromosome. Such a condition is known as *linkage* and will be discussed later.

MODIFIED TWO-GENE RATIOS—DOMINANCE LACKING

We have seen above that, if two genes which determine different characters are located in different chromosomes and one of the members of each pair of genes is dominant over its allele, we will secure a 9:3:3:1

ratio when we cross two F_1 dihybrids to get the F_2 generation, and that the same ratio holds if the two genes control only one character (comb pattern in poultry).

However, if one pair of genes lacks dominance, we would not get a 9:3:3:1 but a 3:6:3:1:2:1 ratio, because the first phenotype containing 9 individuals breaks up into phenotypes containing 3 and 6 individuals each; whereas the third phenotype containing 3 individuals breaks up into two phenotypes containing 1 and 2 individuals each. The following figure will be useful in explaining all of the various modifications of the 9:3:3:1 ratio.

Aa Bb × *Aa Bb*

Eggs	Sperm			
	AB	*Ab*	*aB*	*ab*
AB	*AA BB*(1)	*AA Bb*(5)	*Aa BB*(9)	*Aa Bb*(13)
Ab	*AA Bb*(2)	*AA bb*(6)	*Aa Bb*(10)	*Aa bb*(14)
aB	*Aa BB*(3)	*Aa Bb*(7)	*aa BB*(11)	*aa Bb*(15)
ab	*Aa Bb*(4)	*Aa bb*(8)	*aa Bb*(12)	*aa bb*(16)

FIG. 80.—Generalized checkerboard of a two-gene cross.

If we crossed a polled,[1] red animal, *AA BB*, with a horned, white one, *aa bb*, the F_1 would be polled and roan,[2] *Aa Bb*, assuming gene *A* for polled to be dominant over gene *a* for horns, but gene *B* for red not to be dominant over gene *b* for white, the presence of both *B* and *b* giving the roan color. Then we would have in Fig. 80.

Squares (1), (3), and (9) .... 3 polled, red.
Squares (2), (4), (5), (7), (10), and (13) ..... 6 polled, roan.
Squares (6), (8), and (14) .... 3 polled, white.
Square (11) .... 1 horned, red.
Squares (12) and (15) .... 2 horned, roan.
Square (16) .... 1 horned, white.

If dominance were lacking in both pairs of genes, as it is in a cross between a red-flowered broad-leaved (*AA BB*) and a white-flowered narrow-leaved (*aa bb*) snapdragon, for the F_1 is pink-flowered with leaves of intermediate width, then the F_2 would comprise *AA* red, *Aa* pink, *aa* white, *BB* broad, *Bb* intermediate, *bb* narrow (see Fig. 80), and we would have in the F_2

[1] We are departing from our usual notation in order to be able to use one figure of reference for all the types of variation due to lack of dominance and epistasis.

[2] Dominance between red and white color lacking.

1 red, broad (square 1).
2 pink, broad (squares 3 and 9).
2 red, intermediate (squares 2 and 5).
4 pink, intermediate (squares 4, 7, 10, 13).
1 red, narrow (square 6).
2 pink, narrow (squares 8 and 14).
1 white, broad (square 11).
2 white, intermediate (squares 12, 15).
1 white, narrow (square 16).

or a 1:2:2:4:1:2:1:2:1 ratio.

Breeding results with both plants and animals have revealed several characters that behave in inheritance as though they were controlled by two pairs of genes but do not follow the usual pattern as evidenced in comb type in poultry described earlier in this chapter where the mating of rose-combed birds (*RR pp*) with pea-combed birds (*rr PP*) gave an F_1 of all walnut combs (*Rr Pp*) and an F_2 of 9 walnuts, 3 rose, 3 pea, and 1 single comb. In order to explain these deviating results, the principle of epistasis has been invoked. Again the student is reminded that the *modus operandi* of genetics is to get the results first by breeding plants and animals, and, after the results are secured, to devise a theory which will provide a rational and logical interpretation for the breeding results.

Epistasis is the same relation between pairs of different genes that dominance is between different single genes of one pair of alleles, *i.e.*, gene *A* may be dominant over its allele *a*, or, in an epistatic sense, gene *A* may be dominant over genes *B* or *b* (dominant epistasis), or genes *aa* may be dominant over genes *B* or *b* (recessive epistasis), or both these conditions may hold at the same time, dominant and recessive epistasis. We may further find cases where duplicate dominant, duplicate recessive or incompletely duplicate epistasis may prevail.

Recessive Epistasis.—If we mate a black rat, *AA BB* (gene *A* for color, genes *aa* diluted color, gene *B* for expression of any color, genes *bb* masking all color, *i.e.*, epistatic to *A*) to an albino rat, *aa bb*, all of the F_1 are black, *Aa Bb*, whereas the F_2 will appear as 9 blacks, 3 creams, and 4 whites. This is due to the fact that the presence of at least one *A* and one *B* produces black (squares 1, 2, 3, 4, 5, 7, 9, 10, and 13, Fig. 80), *a*'s and at least one *B* produce cream (squares 11, 12, and 15, Fig. 80), whereas either *AA*, *Aa*, or *aa*, together with *b*'s (squares 6, 8, 14, and 16, Fig. 80), produce albino. This is because the *b*'s mask the expression of *A* or *a*; *i.e.*, *b* is epistatic to *A* or *a*, so that two portions of the usual 9:3:3:1 ratio are thrown together phenotypically. Genes in this relation are sometimes called *supplementary*.

Incompletely Duplicate Epistasis.—Another manifestation of epistasis is one that throws the two middle portions of the 9:3:3:1 ratio together

phenotypically. An example of this occurs in Duroc-Jersey swine, where one sandy-colored race is $AA\ bb$ and another $aa\ BB$. When crossed the F_1 are all red, $Aa\ Bb$, and in the F_2 all the offspring, which get at least one A and one B (squares 1, 2, 3, 4, 5, 7, 9, 10, and 13, Fig. 80), are red, those getting neither A nor B (square 16) are white, and all the others, getting at least one A with b's or at least one B with a's, are sandy (squares 11, 12, 15, 6, 8, and 14, Fig. 80). These are sometimes called *mutually supplementary genes*. A similar case in plants has been found in the fruit shape of squash, where genes A and B together give disk shape, genes AA or Aa with bb and genes aa with BB or Bb give spherical shape, and the double recessive genes give elongated shape.

Dominant Epistasis.—It has been found that a certain type of white dogs, $AA\ BB$ (with color in the eyes), if mated to brown dogs, $aa\ bb$, produce all white offspring, and that, when these F_1 are mated, the peculiar ratio of 12:3:1 appears in F_2. This apparently is due to the white dog carrying color factors (A) that are inhibited from forming color in the hair by another gene (B). The brown dogs lack the gene for black color A, being therefore brown in color, for they also lack the inhibitor B. The F_1 cross is $Aa\ Bb$ and is white because of the dominant epistatic effect of gene B over gene A or a, whereas in the F_2 all those squares that get at least one B (1, 2, 3, 4, 5, 7, 9, 10, 11, 12, 13, and 15, Fig. 80), are white, those getting b's and at least one A (squares 6, 8, and 14, Fig. 80) being black, and the remaining (square 16), $aa\ bb$, being brown. Genes that behave in this fashion are often called *inhibitors*.

Other Types of Epistasis.—Further types of epistasis that the student can work out by means of Fig. 80 are:

Duplicate Recessive Epistasis. aa epistatic to BB, Bb, or bb.
bb epistatic to AA, Aa, or aa.

Sweet peas: white pea $AA\ bb \times$ white pea $aa\ BB$.
F_1 $Aa\ Bb$, all purple.
F_2 9 purple:7 white.

Homo sapiens: deaf person $AA\ bb \times$ deaf person $aa\ BB$.
F_1 $Aa\ Bb$, all normal hearing.
F_2 9 normal hearing:7 deaf.

Duplicate Dominant Epistasis. A epistatic to BB, Bb, or bb.
B epistatic to AA, Aa, or aa.

Poultry: feathered shanks $AA\ BB \times$ clean shanks $aa\ bb$.
F_1 $Aa\ Bb$, all feathered shanks.
F_2 15 feathered shanks:1 clean shanks.

Shepherd's-purse (Bursa): triangular seed pod $AA\ BB \times$ top-shaped seed pod $aa\ bb$.
F_1 $Aa\ Bb$, all triangular seed pods.
F_2 15 triangular seed pod:1 top-shaped seed pod.

Dominant and Recessive Epistasis. *aa* epistatic to *BB*, *Bb*, or *bb*.
B epistatic to *AA*, *Aa*, or *aa*.

Poultry: White Leghorn *AA BB* × White Wyandotte *aa bb*.

F_1 *Aa Bb*, all white.

F_2 13 white:3 colored birds.

Summary on Epistasis.—We have seen from the above examples that the usual two-gene phenotypic ratio of 9:3:3:1 may be modified in a variety of ways by dominance between individual genes in an allelic pair and by various epistatic manifestations between pairs of genes.

The following diagram brings all the above facts into one complete whole.

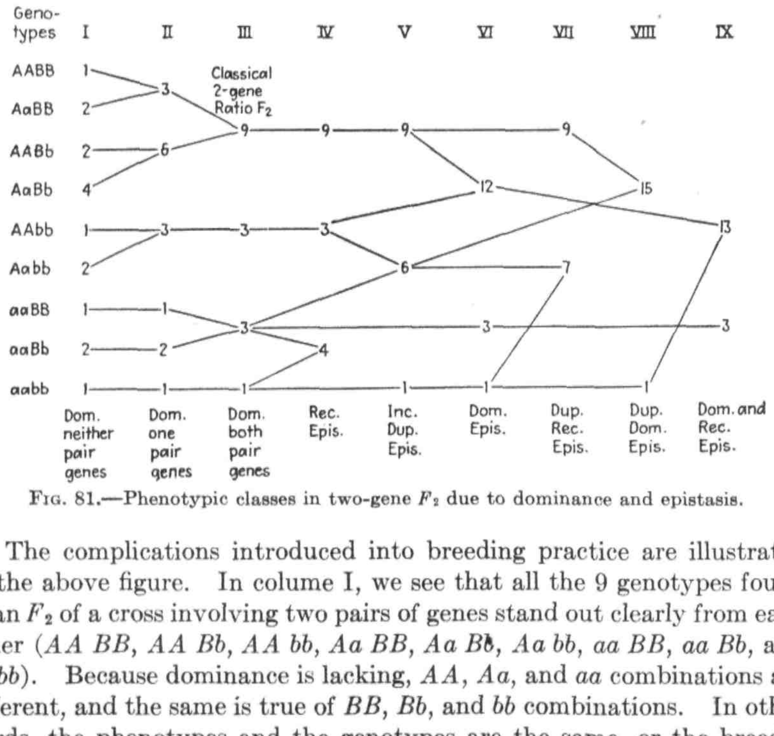

FIG. 81.—Phenotypic classes in two-gene F_2 due to dominance and epistasis.

The complications introduced into breeding practice are illustrated in the above figure. In colume I, we see that all the 9 genotypes found in an F_2 of a cross involving two pairs of genes stand out clearly from each other (*AA BB*, *AA Bb*, *AA bb*, *Aa BB*, *Aa Bb*, *Aa bb*, *aa BB*, *aa Bb*, and *aa bb*). Because dominance is lacking, *AA*, *Aa*, and *aa* combinations are different, and the same is true of *BB*, *Bb*, and *bb* combinations. In other words, the phenotypes and the genotypes are the same, or the breeder knows the genotype when he sees the phenotype. Dominance makes its appearance in one pair of genes (*A*) in column II with the result that *AA BB* and *Aa Bb* can no longer be separated by phenotypic inspection but must be subjected to breeding trials to ascertain their genetic make-up. Similarly, *AA Bb* and *Aa Bb* are now indistinguishable phenotypically, etc. The 9 genotypes of column I have been reduced to 6 phenotypes in column II and are further reduced to 4 in column III. Likewise

further reduction of the 9 original phenotypes of column I to various combinations of 3 and 2 genotypes in columns IV to IX are indicated. Dominance and epistasis complicate breeding practice, because they hide two or several genotypes in one phenotype.

It should be remembered also that we are here dealing with a comparatively simple thing, because it involves only two pairs of genes. If three pairs of genes were acting on the same character and there was no dominance, we would get a phenotypic ratio of 27:9:9:9:3:3:3:1 in the F_2. It is not difficult to imagine the complications that dominance and epistasis would introduce into this situation, and it appears likely that the commercially valuable characters of our larger farm animals were influenced by dozens or hundreds of genes.

Two things are apparent: (1) the scientific livestock breeders need a thorough knowledge of the basic principles of hereditary transmission as worked out with small laboratory animals; and (2) the breeder of the larger animals finds little opportunity to apply this detailed knowledge to his own immediate problems but is forced to devise his own methods of selection and improvement on the basis of the broad principles that have been ascertained through the breeding of laboratory animals.

Analysis of Coat Colors in Mice.

A thorough study of the variations in a group of related characters in any organism will usually reveal an intricate series of interactions between the component factors. As an example we shall choose the house mouse, for in this animal a large number of spontaneous variations have provided the opportunity for a genetic analysis of the factors affecting coat color. Many such factors have been studied and their interrelationships made out. *C* is the fundamental color factor, necessary for the production of any pigment in the coat. Another factor, *A*, or gray, determines the development of the agouti pattern. Its recessive allele, *a*, is present in the nonagouti mice, such as blacks or browns. Still another, *B*, governs the development of black pigment and is dominant over its allelic condition of brown or chocolate, *b*. Many varieties are spotted with white in a blotched or piebald pattern, and such mice contain a factor, *s*, which is recessive to self or solid color, *S*. Another factor, *d*, brings about a clumping of the black and brown pigment granules in the hairs and makes these colors appear faded or dilute, as opposed to the normal fully pigmented form, *D*. Another factor reduces the amount of black and brown pigment in the fur, giving it a pale and washed-out appearance, and also reduces the pigment in the iris, making the eyes appear reddish or pink like the eyes of albinos. The factor, which is called pink eye (*p*) from its most noticeable effect, is recessive to the normal dark-eyed intense-colored condition, *P*. These factors all segregate sharply and may occur in any combination. There are also several other factors affecting coat color which will be omitted for the sake of simplicity. Some of these combinations result in characters which are distinctive and have been given names of their own. Thus the nonblack agoutis are called "cinnamon"

or brown agouti; the dilute blacks, "blue"; the dilute browns, "silver fawn"; and so on. Table 19 lists these various factor combinations, together with the type of coat color produced by each.

TABLE 19.—INTERACTION OF FACTORS FOR COAT COLOR IN MICE

Factors						Gametic formula	Phenotype
C	*A*	*B*	*D*	*P*	*S*	*CABDPS*	Wild-type agouti
					s	*CABDPs*	Spotted agouti
				p	*S*	*CABDpS*	Pink-eyed agouti
					s	*CABDps*	Pink-eyed, spotted agouti
			d	*P*	*S*	*CABdPS*	Dilute agouti
					s	*CABdPs*	Spotted, dilute agouti
				p	*S*	*CABdpS*	Pink-eyed, dilute agouti
					s	*CABdps*	Pink-eyed, spotted, dilute agouti
		b	*D*	*P*	*S*	*CAbDPS*	Cinnamon
					s	*CAbDPs*	Spotted cinnamon
				p	*S*	*CAbDpS*	Pink-eyed cinnamon
					s	*CAbDps*	Pink-eyed, spotted cinnamon
			d	*P*	*S*	*CAbdPS*	Dilute cinnamon
					s	*CAbdPs*	Spotted, dilute cinnamon
				p	*S*	*CAbdpS*	Pink-eyed, dilute cinnamon
					s	*CAbdps*	Pink-eyed, spotted, dilute cinnamon
	a	*B*	*D*	*P*	*S*	*CaBDPS*	Black
					s	*CaBDPs*	Spotted black
				p	*S*	*CaBDpS*	Pink-eyed black
					s	*CaBDps*	Pink-eyed, spotted black
			d	*P*	*S*	*CaBdPS*	Dilute black
					s	*CaBdPs*	Spotted, dilute black
				p	*S*	*CaBdpS*	Pink-eyed, dilute black
					s	*CaBdps*	Pink-eyed, spotted, dilute black
		b	*D*	*P*	*S*	*CabDPS*	Brown
					s	*CabDPs*	Spotted brown
				p	*S*	*CabDpS*	Pink-eyed brown
					s	*CabDps*	Pink-eyed, spotted brown
			d	*P*	*S*	*CabdPS*	Dilute brown
					s	*CabdPs*	Spotted, dilute brown
				p	*S*	*CabdpS*	Pink-eyed, dilute brown
					s	*Cabdps*	Pink-eyed, spotted, dilute brown
c	with any other factors					*c*	Albino, may be of any of 32 genotypes above

All of these types are recessive to the wild coat and appear to have arisen from it by mutation of one or more factors. Thus at any time the wild type may

be reconstituted by bringing into combination all of the alleles of the factors which are responsible for these new types. In fact, the wild coat color itself is found to depend on the presence and interaction of all of the factors named. Thus, in order to produce the agouti pattern there must be present the factors for

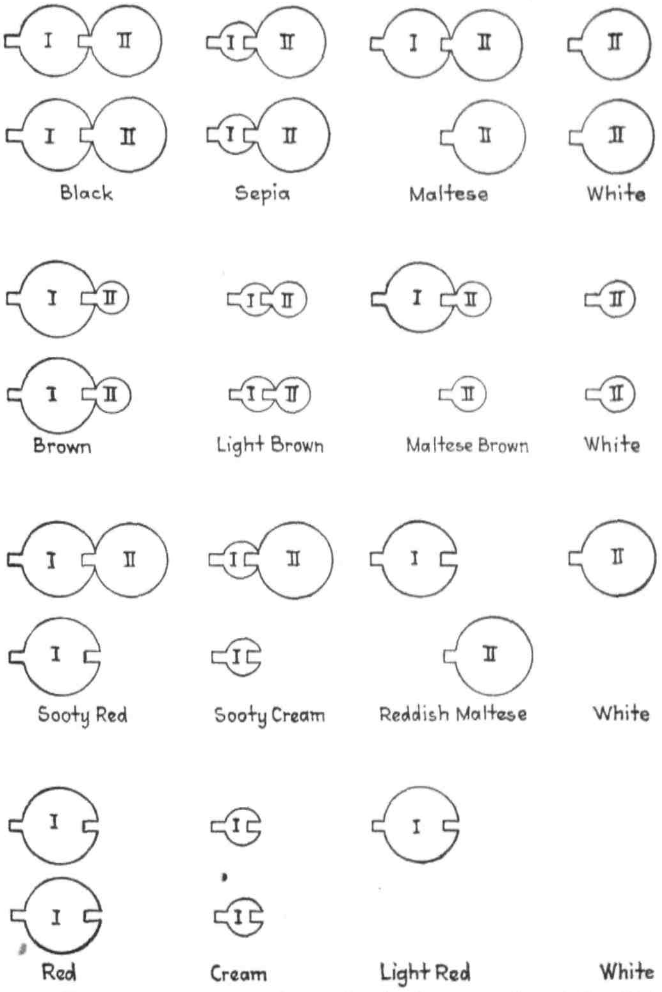

FIG. 82.—Enzymatic action in color production in mammals. (*After Wright.*)[1]

color (C), agouti (A), black (B), dark eye (P), dense color (D), and solid color (S). With regard only to these factors the genotype of the wild mouse may be written $AA\ BB\ CC\ DD\ PP\ SS$. These factors all show essentially complete dominance, so that their heterozygous condition will give the same result as is produced by the homozygous form here given. Thus an animal with the genotype $Aa\ Bb\ Cc\ Dd\ Pp\ Ss$ would also be agouti in appearance. The factors named do not include all that are known, nor is it believable that more than a small sample of the

[1] WRIGHT, S., Production of Coat Color in Mammals, *Jour. Heredity*, **8**: 230, 1917.

factors affecting coat color in mice have been studied. Were knowledge complete, it is probable that the list of factors necessary for the production of the agouti pattern would be much longer and that the letters of the alphabet would be exhausted in attempting to write the genotype of the wild mouse. Here, then, is a clear and convincing example of factor interaction. In order that the apparently simple pattern characteristic of wild house mice may be developed, there must be present at least six factors (probably many more) each of which has a definite effect on coat color. If any single factor is missing or changed, a coat pattern differing more or less widely from the wild type results.

This type of factor interaction is not exceptional but is found whenever numerous variations in a single aspect of the organism are carefully analyzed. Such analyses have been made for several groups of characters in maize. More than a dozen factors affecting the color of the plant are known. The normal color is green, which, like the agouti pattern of mice, results from the combined action of the alleles of all these factors. If one factor is changed, the plant is white instead of green; if another changes, the leaves become red or purple in the sun; whereas changes in various other factors produce brown, yellow, and various combinations of these colors in striped or blotched patterns. In fact, it may be accepted as a general rule that the characters of a plant or animal depend on multiple and finely balanced interactions between a very large number of factors.[1]

Ibsen has made an extended study of the inheritance of coat colors in cattle.[2] It was found necessary to postulate about 25 genes to account for the now known color patterns in our domestic cattle. This example serves to show the extreme complexity of the problem of inheritance in our larger animals. It is undoubtedly even more complex in regard to their commercially valuable qualities. Who would dare even to guess how many genes may be involved in the final expression of the amount of milk a cow may yield to say nothing of the environmental influences involved in such a matter? We can be fairly sure of the fact that many, many genes are involved in determining the characteristics of our livestock, and we can be very sure that they behave in ways comparable to those used as illustrations of different types of inheritance in this and the following few chapters of this book. It may be that we will never know the exact number and interrelations of the genes involved in milk production. Nevertheless, it should be possible to improve our breeding practices on the basis of the general principles involved in the hereditary transmission of characteristics.

Aspects of Dominance.—In the early part of the twentieth century, soon after the rediscovery of Mendel's laws of inheritance, there was a tendency toward oversimplification of the theory. That is to say, there was a tendency to think of each potentiality as determined by one gene

[1] SINNOTT, EDMUND W., and DUNN, L. C., "Principles of Genetics," pp. 98–100, McGraw-Hill Book Company, Inc., New York, 1939.

[2] IBSEN, A. H. L., Cattle Inheritance (Color), *Genetics*, **18**: 441–480, September, 1933.

only. We are now aware of the fact that, rather than one gene's determining a potentiality, many or all of the genes (together with the environment) interact to bring the potentiality to full fruition, though, of course, one gene may still determine the appearance or nonappearance of a definite potentiality.

In like manner the idea of dominance held full sway in the early days of genetics. We now recognize that dominance is a relative rather than an absolute term. For example, brown eyes in man are dominant over blue, but the blue-eyed condition is in turn dominant over red or pink eyes (albinism). Whether blue eyes are dominant or recessive depends therefore on what the characteristic is to which they are being contrasted. There are varying degrees of dominance, from complete dominance to an entire lack of dominance.

The results from crossing tall and dwarf peas; smooth, black and rough, white guinea pigs; or polled, black-bodied black-faced and horned, red-bodied white-faced cattle were clear-cut because in every instance one character was wholly dominant over its allele. If, however, a cross is made between a red Shorthorn and a white one, the result is a roan (mixture of red and white hairs) color pattern. Likewise a cross between a black fowl and a white one gives the typical Blue Andalusian pattern, and a cross between red- and white-flowered four-o'clocks gives a pink hybrid. In these cases, dominance is lacking, and hybrids of this sort never breed true to their own phenotypic appearance because their phenotypic character is due to the interaction of two genes, whereas they can transmit only one gene or the other to any one offspring.

The hybrid character is different from either of the parents; *i.e.*, red crossed with white Shorthorn yields roan, and apparently the final expression of this characteristic hinges on one pair of genes. Similarly in poultry, pea-shaped comb and rose-shaped comb are each individually dominant over a single comb, whereas a cross between homozygous rose- and pea-combed birds yields a new comb character, *viz.*, walnut. To explain these facts two sets of alleles must be postulated and the genetic constitution of a single-combed bird becomes *rr pp*, whereas a pure rose is *RR pp* and a pure pea *rr PP*. These genes (*R* and *P*) are evidently located on different chromosomes, are therefore inherited separately, or according to the law of independent assortment, but act together in producing the final expression of the comb characteristic. If we cross pea-combed and rose-combed birds, the F_1 will all be walnut-combed and the F_2 will give the usual 9:3:3:1 hybrid ratio, (walnut, rose, pea, single).

Dominance may at times be quite variable, depending upon the presence or absence of certain supplementary genes, and, finally, a characteristic may act as a dominant in one sex (baldness in man) and as a

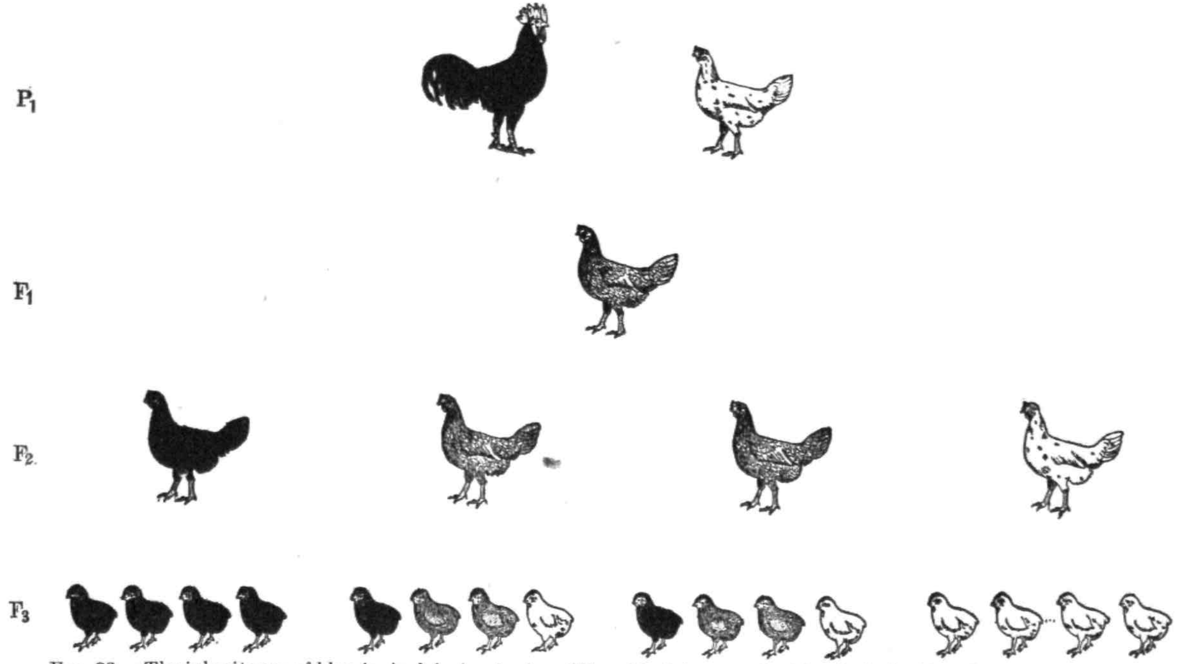

FIG. 83.—The inheritance of blue in Andalusian fowls. When black is crossed with splashed white all the F_1 birds are *blue*. These, if bred together, produce ¼ black, which breed true; ½ blue, which breed like the F_1 blue; and ¼ white, which breed true.

recessive in the other. It is seen, therefore, that the idea of dominance is not the simple thing it was at one time supposed to be.

Occurrences such as the roan pattern in Shorthorn cattle were formerly often spoken of as *blending inheritance*, though the term went out of use as the discrete, atomic nature of the genes became probable. The fact that, when large races of animals are crossed with small ones, offspring result which are intermediate in size induces some still to speak of these offspring as being a *blend* of the two parent races. In terms of chromosomes and genes, of course, they are, but it is now fairly apparent that most of the commercially valuable characters of our animals are determined by the interaction of scores or hundreds of genes rather than by one or two pairs. In this sense, such crossing does result from a blending of many genes, although the genes themselves remain discrete bodies. Dominance generally behaves in the same manner in closely related species, and in most mammals the albino (recessive) gene is the same. However, a characteristic that is dominant in one species may be recessive in another, *e.g.*, black is dominant over white in guinea pigs, but in farm pigs we have learned by experience that white is dominant over black. The expression of dominance may also be influenced by the environment, age, sex, and by other genes in the organism. In short, dominance is variable with many gradations.

The nature of the recessive condition has also been a much-debated question. Some authorities claimed that the recessive gene was a definite entity, others that the recessives indicated losses of genes. T. H. Morgan has adduced evidence from several sources which indicates that recessives are not due to losses of genes; *e.g.*, the fact that albino rats always have a few colored hairs on the feet, that the wings of fruit flies attain considerable length if the temperature is held at 31°C. even though the flies be genetically pure recessive vestigials, and that small eyes appear in old cultures of Drosophila that are pure eyeless recessives. He also cites the fact that certain recessive mutations have been known to revert to the original dominant condition and finally that there are more than a dozen known mutants of eye color in Drosophila at the same locus. From this evidence, it would seem that recessives are caused by the action of definite entities (genes) just as are dominant characteristics and that the idea of considering recessives as losses of genes is an untenable one.

The student should try to appreciate fully that the facts of breeding came first, theories to explain them second. Genetics is but a systematic arrangement of breeding facts together with theories that offer a logical explanation. Any theory must do two things: (1) explain past facts and (2) allow us to prognosticate. All of the theories of genetics to be discussed later are backed by a multitude of fact. As soon as a new fact is

discovered which cannot be fitted into the presently accepted theory, that theory will have to be supplanted by one which will accommodate all the old plus the new facts. This revision of theory has been necessary many times in the past short life of genetics.

Summary.—In this chapter we have become acquainted with some of the simpler but basic principles of heredity. We have learned that heredity is referable to paired, particulate bodies called *genes*, located in the chromosomes. We have seen that these genes retain their identity at all times whether expressed phenotypically or not. We are now familiar with two of the basic laws of heredity, *viz.*, segregation and independent assortment of the chromosomes. The latter exist in pairs, and one complete set (haploid, n) is given to each offspring by each of its parents through an egg or a sperm, which makes each offspring diploid or $2n$. This offspring in turn passes on a random sample of its chromosomes, one of each pair, however, to each of its offspring. We traced this procedure where one, two, or three pairs of genes in separate chromosomes were involved. We learned the F_2 monohybrid ratio to be 3:1 phenotypically (or 1:2:1 genotypically) and the F_2 dihybrid ratio to be 9:3:3:1 phenotypically. Finally, we studied various modifications of the two-gene ratio due to lack of dominance between alleles or between pairs of genes, the latter condition being known as *epistasis*, and attempted to clarify our minds regarding several aspects of dominance and recessiveness.

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Problems[1]

The following problems are designed to promote facility in correct genetic thinking. Not until you can work these and similar problems quickly and correctly will you have a comprehensive grasp of the genetic principles that they illustrate.

1. If a homozygous rough-coated animal is crossed with a smooth one, what will be the appearance of the F_1? Of the F_2? Of the offspring of a cross of the F_1 back on its rough parent? On its smooth parent?

2. A certain rough-coated guinea pig bred to a smooth one gives 8 rough and 7 smooth offspring. What are the genotypes of parents and offspring?

3. If one of the rough F_1 animals in the preceding question is mated to its rough parent, what offspring may be expected?

4. Two rough-coated guinea pigs when bred together produce 18 rough and 1 smooth offspring. What are the genotypes of the parents?

5. Cross a homozygous rough, black animal with a smooth, white one. What will be the appearance of the F_1? Of the F_2? Of the offspring of a cross of the F_1 back with the rough, black parent? With the smooth, white one?

[1] These problems and those at the ends of the next two chapters are taken for the most part from lists in Sinnott and Dunn, "Principles of Genetics," McGraw-Hill Book Company, Inc., New York, 1939, and are reproduced here through the kind permission of the authors.

6. In the F_2 generation in the preceding question, what proportion of the rough, black individuals may be expected to be homozygous for both characters?

7. NOTE.—Polled or hornless condition in cattle (P) is dominant over horned (p).

A certain polled bull is bred to three cows. With cow A, which is horned, a horned calf is produced; with cow B, also horned, a polled calf is produced; and with cow C, which is polled, a horned calf is produced. What are the genotypes of all these four animals and what offspring would you expect from these three matings?

8. NOTE.—In Shorthorn cattle the heterozygous condition of red coat color (R) and white (W) is roan.

If two roan Shorthorn cattle are mated, what chance will their offspring have of resembling their parents in coat color?

9. Two black female mice are crossed with a brown male. In several litters female No. 1 produced 9 blacks and 7 browns; female No. 2 produced 17 blacks. What deductions can you make concerning inheritance of black and brown coat color in mice? What are the genotypes of the parents in this case?

10. A breeder has a group of animals all of which are heterozygous for a given dominant character, A, and thus have the genotype Aa. He wants to establish a race homozygous for A. To accomplish this he allows these animals to interbreed freely and then practices mass selection among their offspring, saving for breeding all individuals that show the character A and discarding only the aa animals. Members of one generation do not cross with any other. In the third generation, what proportion of the animals which have the character A will be homozygous for it? How could the breeder have established a homozygous strain more easily?

11. If the breeder mentioned in the previous question is practicing mass selection for two characters, A and B, and his original animals have the genotype $Aa\ Bb$, would selection be effective more rapidly or more slowly than when only one character was concerned? Explain.

12. It has long been known that Blue Andalusian fowls do not breed true to the blue color of their plumage. How do you explain this?

13. What offspring will a Blue Andalusian fowl have if bred to birds of the following plumage colors: (1) black, (2) blue, (3) white?

14. NOTE.—In man, brown eyes (B) are dominant over blue (b). A brown-eyed man marries a blue-eyed woman and they have 8 children, all brown-eyed. What are the genotypes of all the individuals in the family?

15. A blue-eyed man both of whose parents were brown-eyed marries a brown-eyed woman whose father was brown-eyed and whose mother was blue-eyed. They have one child, who is blue-eyed. What are the genotypes of all the individuals mentioned?

16. Assume that in man, right-handedness (R) is dominant over left-handedness (r). A right-handed man whose mother was left-handed marries a right-handed woman who has three brothers and sisters, two of whom are left-handed. What chance will the children of this marriage have of being left-handed?

17. What are the chances that the first child from a marriage of two heterozygous brown-eyed parents will be blue-eyed? If the first child is brown-eyed, what are the chances that the second child will be blue-eyed?

18. At the time of synapsis preceding the reduction division, the homologous chromosomes align themselves in pairs and one member of each pair passes to each of the daughter nuclei. Assume that in an animal with four pairs of chromosomes, chromosomes A, B, C, and D have come from the father and A', B', C', and D' have come from the mother. In what proportion of the germ cells of this animal will all of the material chromosomes be present together? All of the paternal?

19. If one individual is homozygous for four dominant factors and another for their four recessive allelomorphs, and if these two individuals are crossed, what proportion of the F_2 from this cross will resemble each parent, respectively, in appearance?

20. A rough, black guinea pig bred with a rough, white one gives 28 rough, black; 31 rough, white; 11 smooth, black; and 9 smooth, white. What are the genotypes of the parents?

21. Two rough, black guinea pigs when bred together have 2 offspring, one of them rough, white and the other smooth, black. If these same parents were to be bred together further, what offspring would you expect from them?

22. If a homozygous polled, white animal is bred to a horned, red one, what will be the appearance of the F_1? Of the F_2? Of the offspring of a cross of the F_1 back with the polled, white parent?

23. A polled, roan bull bred to a horned, white cow produces a horned, roan daughter. If this daughter is bred back to her father, what offspring may be expected as to horns and coat color?

24. In swine, white coat is dominant over black and the "mule-footed" condition over that with normal feet. A white, mule-footed boar, A, always produces white, mule-footed offspring, no matter to what sow he is bred. Another boar, B, however, also white and mule-footed, when bred to black sows produces about ½ white and ½ black offspring, and when bred to normal-footed sows, about ½ mule-footed and ½ normal offspring. Explain this difference between these two animals by comparing their genotypes for these two traits.

25. In poultry, feathered legs (F) are dominant over clean legs (f); and pea comb (P) over single comb (p).

Two cocks, A and B, are bred to two hens, C and D. All four birds are feathered-legged and pea-combed. Cock A with both hens produces offspring that are all feathered and pea. Cock B with hen C produces both feathered and clean, but all pea-combed, but with hen D produces all feathered but part pea-combed and part single. What are the genotypes of these four birds?

26. In poultry, the factors for rose comb (R) and pea comb (P), if present together, produce walnut comb. The recessive allelomorphs of both, when present together in a homozygous condition, produce single comb.

What will be the comb character of the offspring of the following crosses, in which the genotypes of the parents are given?

$Rr\,Pp \times Rr\,Pp$	$Rr\,Pp \times Rr\,pp$
$RR\,Pp \times rr\,Pp$	$Rr\,pp \times rr\,Pp$
$rr\,PP \times Rr\,Pp$	$Rr\,pp \times Rr\,pp$

27. In the following five questions, all of which concern comb form in poultry, determine the genotypes of the parents:

A rose crossed with a walnut produces offspring ⅜ of which are walnut, ⅜ rose, ⅛ pea, and ⅛ single.

28. A walnut crossed with a single produces offspring ¼ of which are walnut, ¼ rose, ¼ pea, and ¼ single.

29. A rose crossed with a pea produces 6 walnut and 5 rose offspring.

30. A walnut crossed with a single produces 1 single-combed offspring.

31. A walnut crossed with a walnut produces 1 rose, 2 walnut, and 1 single offspring.

32. If one of the walnut parents in the preceding question were crossed with one of its single-combed offspring, what would their offspring be like?

33. A rose crossed with a walnut produces offspring $\frac{3}{8}$ of which are walnut, $\frac{3}{8}$ rose, $\frac{1}{8}$ pea, and $\frac{1}{8}$ single. What are the genotypes of the parents?

34. A feather-shanked rose-combed crossed with a clean-shanked pea-combed one produces 25 feather, pea, offspring; 24 feather, walnut; 26 feather, rose; and 22 feather, single. What are the genotypes of the parents?

35. The offspring of a feather-legged pea-combed cock bred to a clean-legged pea-combed hen are all feather-legged. Most of them are pea-combed, but some singles appear among them. What are the genotypes of the parents? What would be the offspring expected from a cross of this hen with one of her feather-legged single-combed sons?

36. A right-handed blue-eyed man whose father was left-handed marries a left-handed brown-eyed woman from a family in which all the members have been brown-eyed for several generations. What offspring may be expected from this marriage, as to the two traits mentioned?

37. A brown-eyed right-handed man marries a blue-eyed right-handed woman. Their first child is blue-eyed and left-handed. If other children are born to this couple, what will probably be their appearance as to these two traits?

38. A right-handed blue-eyed man marries a right-handed brown-eyed woman. They have two children, one left-handed and brown-eyed and the other right-handed and blue-eyed. By a later marriage with another woman who is also right-handed and brown-eyed, this man has 9 children all of whom are right-handed and brown-eyed. What are the genotypes of this man and his two wives?

39. A brown-eyed normal-minded man marries a brown-eyed normal-minded woman. Their first child is blue-eyed and feeble-minded. What is the chance that the next child will also show these same characteristics? (Normal mind, dominant.)

40. A breeder has a homozygous race of feather-legged, black, rose-combed birds and another of clean-legged, white, pea-combed ones. He wants a race of black birds that have clean legs and walnut combs. What proportion of the F_2 raised from a cross between these two races will be what he desires in appearance?

41. What are the phenotypes of the parents and offspring of the following cross: *ff Rr Pp* × *Ff Rr pp*.

42. In rabbits there are several factors that determine coat color:

C colored	*c* no color, albino
A ticked, agouti	*a* solid color, nonagouti
B black	*b* brown
S solid color	*s* spotted

(*AB*, agouti; *Ab*, cinnamon; *aB*, black; *ab*, brown)

An albino rabbit mated with a black produces agouti and black, spotted young. What factors are present in the albino parent and not in the black?

43. An agouti animal crossed with another agouti produces offspring of which $\frac{9}{16}$ are agouti, $\frac{3}{16}$ black, $\frac{3}{16}$ cinnamon, and $\frac{1}{16}$ brown. What are the genotypes of the parents?

44. What are the offspring of the following crosses? What are the appearances of the parents?

(*a*) *Cc Aa bb* × *cc aa Bb*
(*b*) *cc Aa Bb* × *CC aa Bb*

45. Two agouti rabbits produce 3 agouti and 1 black offspring. What are their genotypes? (Use only the *A*,*a* and *B*,*b* factors.)

46. In what two ways could you develop a pure-breeding strain of polled, black-bodied white-faced cattle?

47. NOTE.—In cattle the polled condition (*P*) is dominant over the horned (*p*); and in Shorthorns the heterozygous condition of red coat (*R*) and white coat (*r*) is roan.

If a homozygous polled, white animal is bred to a horned, red one, what will be the appearance of the F_1? Of the F_2? Of the offspring of a cross of the F_1 with the polled, white parent? With the horned, red parent?

48. If a group of 100 polled, roan Shorthorn cows by horned bulls were mated to a roan bull that was heterozygous for the polled condition, what sort of offspring would you expect and in what numbers?

49. If a red-flowered broad-leaved plant is crossed with a white-flowered narrow-leaved one, what will be the appearance of the F_1 and the F_2?

50. If in mice you secured a 9 agouti:3 black:4 albino ratio in an F_2, what were the genotypes of the parents and the F_1 using the letter *C* to represent the gene necessary for the expression of any color and *A* to represent the gene for banding of the black hairs with yellow to give the agouti pattern. What type of inheritance is this?

51. In cultivated stocks (a flower) gene *C* in the absence of gene *R*, produces cream-colored flowers; gene *C* with gene *R*, red ones and genes *cc* with *RR*, *Rr*, or *rr* white flowers. If you crossed a red-flowered plant with a white and got an F_1 that was all red, what proportion of red, creams, and white flowers would you get in the F_2.

52. If you cross two spherical-shaped squash and secure a disk-shaped F_1 and then cross one of these F_1's to an elongated-fruit plant, what will be the fruit shape of their offspring?

NOTE.—In summer squashes the factor for white fruit color, *W*, is epistatic to that for yellow, *Y*; *WY* and *Wy* plants are white; *wY* plants yellow, and *wy* plants green.

53. What is the color of the fruit in the offspring of the following crosses, the genotypes of the parents being given?

$$Ww\ Yy \times Ww\ yy \qquad ww\ YY \times Ww\ yy \qquad Ww\ yy \times ww\ Yy$$

NOTE.—In the following three questions, which deal with fruit color in squashes, find the genotypes of the parents.

54. A white plant crossed with a yellow one produces offspring of which ½ are white, ⅜ yellow, and ⅛ green.

55. A white plant crossed with a green one produces offspring of which ½ are white and ½ yellow.

56. A white plant crossed with another white one produces offspring of which ¾ are white, $\frac{3}{16}$ yellow, and $\frac{1}{16}$ green.

57. What will be the flower color of the offspring of the following crosses, in which the genotypes of the parents are given?

$$Cc\,Pp \times cc\,Pp \qquad cc\,Pp \times CC\,pp$$
$$Cc\,Pp \times Cc\,PP \qquad Cc\,pp \times cc\,Pp$$

58. A white-flowered plant crossed with a purple produces offspring of which ⅜ are purple and ⅝ white.

59. A purple-flowered plant crossed with a white one produces offspring of which ½ are purple and ½ white.

60. A white-flowered plant crossed with another white produces offspring of which ¾ are white and ¼ purple.

61. In wheat, determine the genotypes of the parents in the following crosses:

(*a*) Red × white giving ¾ red and ¼ white.
(*b*) Red × red giving ⅞ red and ⅛ white.

62. How would you proceed in developing a feathered-shanked strain of poultry from clean-shanked birds?

63. If an F_2 yields a 15:1 ratio, what could you conclude as to the type of inheritance involved?

64. Write the genetic color formulas for two breeds of poultry both of which are white and the F_2 resulting from their crossing gives a 13 white:3 colored ratio.

65. Starting with two white breeds of poultry, how would you proceed to develop a true-breeding colored strain?

CHAPTER XIV

THE PRINCIPLES OF HEREDITY (*Continued*)

In the preceding sections we have dealt with some of the more simple and clean-cut types of inheritance. During the past 30 years the inheritance of a great many traits in plants and animals has been studied and the methods of transmission from parent to offspring ascertained. The following might be called different types of inheritance, although basically there is but one type of inheritance, *viz.*, by means of genes. This method of inheritance is typical of all sexually reproducing forms, so that what may appear as different types of inheritance are actually different sorts of expressions of gene reactions. The procedure has been to cross plants or animals possessing different characteristics, tabulate the results by separate generations, and, finally, to construct a theory that would fit the observed facts. It should be noted that the facts come first and the theory to explain the facts comes later. This is the scientific approach. In animal breeding, we sometimes find people making the directly opposite approach, *i.e.*, starting out with a theory and trying to find facts that fit their theory. They generally do find some such facts, but unless one takes all the known facts into account, his contribution is apt to be nil. If one "selects" his facts carefully enough he can "prove" almost anything. Several typical forms of inheritance will be presented in the following sections.

Multiple Alleles.—Thus far we have spoken of only two alternatives as far as one pair of genes is concerned. We have talked about gene A or its allele, gene a. We have said, too, that the genes are probably complex, organic molecules made up of hundreds of thousands of atoms arranged spatially in some definite pattern. We assume too that the content and spatial arrangement of the atoms in gene A are different from those in gene a. It would seem logical, therefore, to expect that there might be more than two alternative arrangements. Breeding experience seems to indicate that there are.

If a colored rabbit, CC, is bred to an albino, c^ac^a, all the F_1 are colored, and in the F_2 there are 3 colored:1 albino. Likewise another cross, between colored, CC, and Himalayan, c^hc^h (white with black nose, ears, tail, and feet), gives an F_1 all of which are colored and the familiar 3 colored:1 Himalayan in the F_2. Now, if the cross is made between Himalayan, c^hc^h, and albino, c^ac^a, all the F_1 are Himalayan and in the F_2

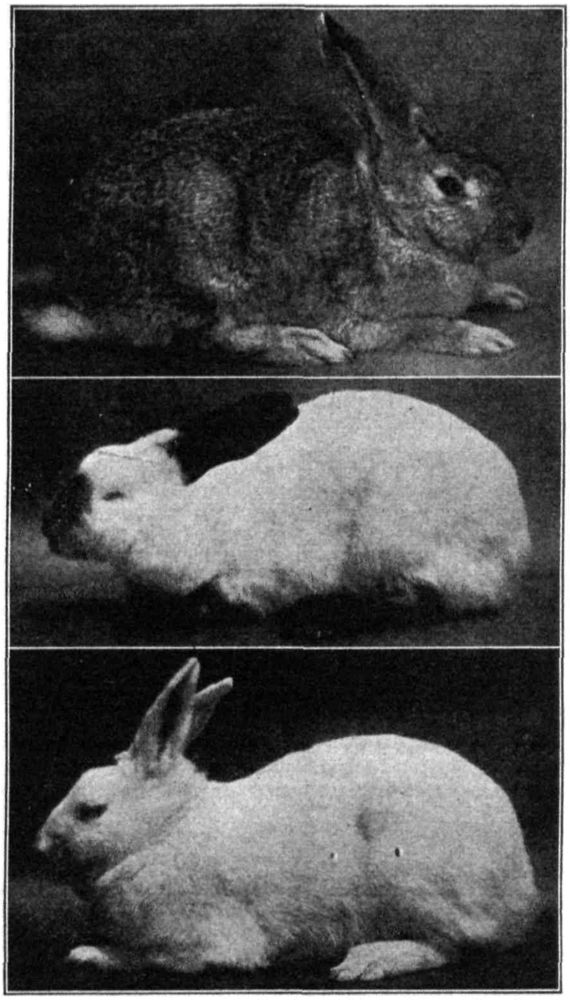


FIG. 84.—Three alleles of a gene for coat color in rabbits. Top, colored; center, Himalay albinism; bottom, complete albinism. (*From Castle, in Journal of Heredity.*)

allelic series. Still another gene, c^{ch}, has been found in this series causi the chinchilla color or silvery gray with no yellow color in the fur, and tl has been found, as far as dominance is concerned, to fit in between gen C and c^h. Thus we could have the following genotypes.

colored rabbit	CC, Cc^{ch}, Cc^{h}, Cc
chinchilla rabbit	$c^{ch}c^{ch}$, $c^{ch}c^{h}$, $c^{ch}c$
Himalayan rabbit	$c^{h}c^{h}$, $c^{h}c$
albino rabbit	cc

Many other multiple allelic series are known in both plants and animals and in most of them dominance between the members below the wild-type dominant is lacking. In mice a multiple allelic series of four genes is known, gene C producing full color; gene c^{ch} dilute color or chinchilla; gene c^{h} extreme dilution; and gene c albinism, or lack of color. Here gene C is dominant over the other members of the series, but crosses between the other members give results intermediate between the two used, *e.g.*, crossing homozygous chinchilla with albino gives the intermediate, extreme dilution. Allelic series are known in many plants, and in Drosophila there are 14 alleles of the gene for red eye grading all the way down to white eyes. Series of multiple alleles are also known in guinea pigs, rats, mice, rabbits, and snapdragons.

In man, blood types show a multiple allelic series of three genes. Blood itself is not inherited, but type of blood is. The red-blood cells in man contain an antigen A or B or both. The blood serum contains antibodies a or b or both. A person of blood group A has antigen A in his red-blood cells and antibody b in his serum; of blood group B has antigen B in his red cells and antibody a in his serum; of blood group AB has antigens A and B in his red cells and neither antibody in his serum; and, finally, a person of blood group O has neither antigen A nor B in his red cells but both antibodies a and b in his blood serum. If, therefore, red cells from a person with the A antigen were introduced by blood transfusion into a person of type B with antibody a in his serum, the reaction between the serum antibody a and the red-cell antigen A would cause these cells to clump or agglutinate with possibly fatal results. In making blood transfusions, blood types must be ascertained in order to prevent red-cell agglutination.

TABLE 20.—BLOOD TYPES IN MAN

Type	Genetic make-up	Antigen in cells	Antibody in serum	Can give blood to	Can take blood from
A	AA or Aa	A	b	A or AB	A or O
B	$A^{B}A^{B}$ or $A^{B}a$	B	a	B or AB	B or O
AB	AA^{B}	AB	o	AB	All
O	aa	o	ab	All	O

Knowledge of the genetic make-up of individuals regarding blood type (Table 20) is sometimes useful in establishing possible, though not actual, paternity. If, for instance, a mother is of type A (genetic

make-up AA or Aa) and her child is of type O (genetic make-up aa thus making mother Aa) and the assumed father turns out to be type AB (genetic make-up AA^B), this fact removes the possibility of his having actually been the child's father, because the child received two a's and no man of type AB has an a to transmit to his offspring. If the tests revealed that the assumed father was of type A, B, or O, then the most that can be said is that he might have been the father as, of course, might also many other men.

Lethal Action of Genes.[1]—Any organism is a delicately balanced system of actions and reactions and can survive only a more or less limited range of change. This is nicely illustrated in the blood stream, which must maintain a proper balance of sugar, minerals, vitamins, hormones, and other elements if the organism is to function normally. All bodily characteristics are referable in the final analysis to the genes, which produced the organism, manifesting themselves of course in our internal and external environment.

It is not surprising, therefore, that gene changes sometimes result in the sort of unbalance that destroys the organism. Such manifestations are known as *lethals*. In the fowl, for instance, there sometimes occurs a condition known as *creeper* (short wings and legs). When two creepers are mated, some normal offspring are produced, the normal condition apparently being recessive to creeper, but the ratio of such matings is 2 creeper: 1 normal. Investigation has shown that some of the embryos die at about the fourth day of incubation, these presumably being homozygous creepers. Creeper, therefore, has the genetic constitution Cc, normal cc, this being a dominant lethal, according to Snyder, and the homozygous and heterozygous conditions are recognizably different.

Several recessive lethals are known in cattle, *viz.*, parrot-beaked (abnormal lower jaw; calves live only a few hours), amputated (calves born dead with legs and lower jaw missing), short-spined (fused and compacted vertebrae), hairless. Bulldog calves with greatly dished faces and very short legs are a dominant lethal manifestation similar to creeper in fowl, the heterozygotes being the short-legged Dexter cattle.

Other abnormal conditions that may be due to lethal genes include mummified calves, resorbed fetuses, ossified joints, and various types of congenital dropsy. Other lethals in farm animals are known, *e.g.*, paralyzed hind limbs in sheep and swine, thick forelimbs, closed anus and cleft palate in swine, closed colon in horses. If an abnormal embryo is born the lethal is made obvious. Such happenings are generally due to

[1] See EATON, O. N., A Summary of Lethal Characters in Animals and Man. *Jour. Hered.*, **28** (9): 320–326, September, 1937.

failure to reach full development; *e.g.*, hair or limbs do not grow; palate, skull, or lips do not fuse in the mid-line; joints fail of full development with fluid and pads between bones. Lethals that destroy the organism in early embryonic life with its subsequent resorption may pass unrecognized as sterility.

Like most other mutations, the bulk of lethals are recessive and may remain hidden in a stock for many generations. For their total removal from a strain, test matings and rigid selection must be practiced with the knowledge that in the case of recessives both parents are carrying the gene.

Many lethals of various sorts are known also in plants and in man. Lethals may kill the organism at any time, *i.e.*, during embryonic, fetal, or postnatal times; and, if the lethal gene is located on the sex chromosome, peculiar sex ratios will of course result.

The following list of lethals contains those listed by Eaton[1] in 1937 and a few others reported in the *Journal of Heredity* since that time.

Horses	
Atresia coli—closure of intestine	R*
Abnormal sex ratio—55 males:90 females ....Sex-linked	R
Lethal white—low fertility—lethal or sterility factors or both	?
Stiff forelegs ....Probably	R
Cattle	
Achondroplasia₁—(Bulldog) short legs and head, hernia, die and aborted fourth month	D†
Achondroplasia₂—(Bulldog) short head, cleft palate, deformed jaws, die soon	R
Acroteriasis congenita—amputated—appendages short or absent	R
Agnathia—very short lower jaw (sex limited to male?)	R
Ankylosis—ossification of joints	R
Congenital dropsy—water in tissues and cavities	R
Congenital ichthyosis—scaly, cracked skin	R
Epitheliogenesis imperfecta—imperfect skin, partly hairless—septicemia	R
Fetal resorption	?
Hernia cerebri—failure of frontal bones to fuse	?
Impacted molars—short jaw, defective teeth—die within week	?
Lameness in hind limbs—calves unable to stand	R
Muscle contracture—head and legs drawn up—joints stiff	R
Mummification—short, stiff neck, prominent joints—usually die as 8 months fetus	R
Short limbs—limbs short, hoofs undeveloped	R
Short spine—ribs and vertebrae fused, back bent down	R

* R = recessive.
† D = dominant.

[1] *Loc. cit.*

Sheep

Amputated—no claws on feet	?
Earless and cleft palate	R
Lethal gray—in Turkanas and Karakuls	R
Muscle contracture—usually stillborn	R
Paralysis—hind parts paralyzed—live few days	R
Skeletal defects—large head, short upper jaw, rigid fetlocks	R

Swine

Atresia ani—closed colon	?
Catlin mark—parietal or frontal bones not fused	R
Cleft palate—young unable to nurse	R
Excessive fatness—young die at 40 to 80 kg	R
Fetal mortality	R
Hydrocephalus—water outside brain in subarachnoid spaces	R
Hypotrichosis—hairless (lack of iodine)	?
Legless—(shoulder blades and pelvic bones but no limb buds or leg bones)	R
Lobed ear—usually also cleft palate and deformed hind legs	Probably R
Muscle contracture—thick, stiff legs	R
Paralysis—hind parts paralyzed	R

Man

Brachyphalangy—short middle phalanx second finger and toe, live 1 year	D
Congenital ichthyosis—cracked, imperfect skin, live 3 days	R
Glioma retinae—malignant tumor of retina	?
Icterus—jaundice, live 4 days to 3½ years	?
Infantile amaurotic idiocy—degeneration of cerebro-spinal nerves, live 2 or 3 years	R
Progressive spinal muscular atrophy—live a few years	?
Xeroderma pigmentosum—sensitive skin, scars, and carcinoma, live 12 years	R

Multiple Factors.—Thus far our discussion has been confined to qualitatively differing characters such as color of hair, presence or absence of horns or of feathers, types of blood, or the ability or inability to survive, etc. There are many other characters, in fact most of the important ones, that do not exhibit this alternative type of expression but rather show all manner of gradation between rather wide limits. Such characters are quantitative and, as examples, size, yield, power, stamina, rapidity of fattening, quality of carcass, degrees of fertility, and probably most of the other commercially important characters of our livestock might be mentioned.

It seems probable that the final expression of a great many characteristics of higher animals may be due to the interaction of many sets of genes. This point of view has dawned gradually, as more detailed information about inheritance in some of the lower forms of life has accumulated, and is in direct contrast to the views held soon after the

rediscovery of Mendel's work. Attempts have been made to analyze complex physiological processes such as milk production and the percentage of fat in milk on the basis of the interaction of a few pairs of genes, but they have not been successful. Fortunately, it should be possible to make progress in breeding on the basis of a sound knowledge of the basic principles even in the absence of specific information concerning the number and interactions of the genes responsible for the appearance of commercially valuable qualities. When many factors or genes are concerned, we know that the offspring arising from the mating of two extremes tend to fall on the average about midway between two parental levels. This principle is involved in indexing dairy bulls, as described in detail in Chap. XXIII.

The multiple-factor hypothesis grew out of the work of Nilsson-Ehle with wheat and East with corn. The former crossed several strains of red and white wheats. In general the red color was only partially dominant over white, for the F_1 was not as dark red as the red parent. In the F_2 there were 3 reds (1 dark red, 2 lighter red) to 1 white. This indicates a one-gene pair reaction. Another cross of red and white wheats gave a similar F_1 but an F_2 of 15 reds (of varying shades) to 1 white thus indicating a two-gene pair reaction. Still a third cross gave the usual F_1 but an F_2 of 63 reds (again of varying shades) to 1 white, which indicates a three-gene pair reaction. This uniformity of the F_1 and variability of the F_2 is generally true of quantitative characters controlled by many genes. Breeding tests revealed that there were one, two, and three pairs of genes operating in these cases. In the two-gene cross it was shown that a wheat with four red genes was redder than one with three, this latter one redder than one with two, and this in turn redder than a wheat with only one red gene. In these cases, there is not complete dominance, but the genes act in a cumulative fashion.

This method of inheritance is now thought to be operative (along with dominance, epistasis, and other types) in the inheritance of most of the commercially important animal characters. In other words, instead of color of wheat, we might substitute size, weight, yield, or many other quantitative traits. This will explain the difficulties encountered in attempting to unravel the exact mode of inheritance of many characters in the larger animals.

It is possible to determine with a fair degree of accuracy how many genes are operating to produce a given characteristic. If two extremes are mated, the F_1 will fall about midway between the parents if the genes are acting cumulatively. If one out of the four of the F_2 is as extreme as each of the two extreme grandparents, then we are justified in assuming that one pair of genes is involved. If one out of sixteen of the F_2 is as extreme as each grandparent, then two genes must be operative.

This interpretation fits very well the observed reactions of color inheritance in man, black skin being represented by *AA BB* and white skin by *aa bb*. The F_1 will be mulattoes, *Aa Bb*, and will yield five grades of color depending on the number of dominant genes present, *AA BB* being black, *AA Bb*, etc. being dark brown, *Aa Bb*, etc. being mulatto, *Aa bb*, etc. being light brown, and *aa bb* white.

A cross between long-eared rabbits (220 mm.) and short-eared (100 mm.) gives offspring with ears about 160 mm. in length. These F_1 rabbits in turn produce a graded scale of ear lengths in F_2 ranging from 220 down to 100 mm., each dominant gene accounting for an increased ear length of 20 mm. and acting cumulatively. The student should make up a table showing the number of operating genes on the basis of the number of extreme individuals in the F_2 and will find such a table useful in interpreting problems involving cumulative multiple-factor inheritance; 1 out of 4 as extreme as each grandparent = 1 pair of genes; 1 out of 16 = 2 pairs, 1 out of 64 = 3 pairs, etc.

On the basis of multiple-factor inheritance it is possible to make crosses that will yield some F_2 members more extreme than either grandparent. This is probably due to each parent contributing some effective alleles not supplied by the other parent and is known as *transgressive variation*. Thus one parent might be *AA BB cc* and the other *aa BB CC*, whereupon the F_1 would be *Aa BB Cc*, but giving the possibility of getting *AA BB CC* in the F_2, which would be more extreme than either grandparent.

Variations based upon the interaction of multiple genes can be analyzed statistically, and an introduction to the general field of statistical analysis will be found in Chap. XVIII.

A question as to the scientific validity of the additive, nondominant action of multiple genes has recently been raised by MacArthur.[1] Using diallel crossing between four varieties of tomatoes with fruit weights ranging from 0.8 g. through 3.6, 65.9, and 106.8 g. per variety, this investigator found that the various F_1 hybrids were not an arithmetic average between the pure parent stocks but closely approached the geometric means of the parental varieties. For example, the cross between the 0.8-g. parent and the 3.6-g. parent did not yield an F_1 of 2.2 g. (the arithmetic mean) but the F_1 averaged 1.7 g. ($\sqrt{0.8 \times 3.6}$). Likewise the cross between the 3.6-g. and the 106.8-g. parents gave an F_1 of 19.4 g. (very close to $\sqrt{3.6 \times 106.8} = 19.6$) rather than the arithmetic mean of 55.2 g. The whole series of crosses was orderly and followed the geometric rather than the arithmetic pattern. The size of the F_1 fruits was quite evidently controlled to a large extent by the genes provided

[1] MacArthur, J. W., Size Inheritance in Tomato Fruits, *Jour. Hered.*, **32** (9): 291–295.

by the smaller parent or, stated differently, the amount of additional growth brought about by the genes of the larger parent was limited in a proportional manner by the substrate upon which the activating substances reacted.

Because so many of the commercially important characters of our livestock are dependent on cell size, cell number, or cell activity and appear to be controlled by many genes, this new theory, if it proves to be of general validity, will have an important bearing on our reasoning and procedures in livestock breeding. If, for example, 4,000-lb. producing cows were mated to a bull with a hereditary complex for 24,000 lb. of milk, we would expect the resulting daughters to average not halfway between 4,000 and 24,000 or 14,000 lb. (the arithmetic mean) but rather at 9,800 lb. ($\sqrt{4,000 \times 24,000}$). In other words, the genes from this very high-heredity sire are limited proportionally by the low heredity genes of the dams. Where the differences in the hereditary levels are small, the arithmetic and geometric means are very similar. For example, if the sire's level was 14,000 lb. and the dams 12,000 lb., the arithmetic mean would be 13,000 and the geometric mean 12,961 lb.

Sex-linked Inheritance.—In the examples used thus far to illustrate various types of inheritance, it has made no difference as to sex where the various characteristics were placed; *i.e.*, this set could have been in the male, that in the female, or vice versa. In the type now to be discussed, however, it will make a difference, because the genes determining the characteristics will be located in the chromosomes that determine the sex of the individual.

Drosophila melanogaster, the common fruit fly, has provided more material assistance than any other species in the solution of the problems involved in hereditary transmission. Cytological studies of the cells of this organism reveal the fact that they have four pairs of chromosomes. In the female, these are all evenly paired, two of the pairs being large, bent rods; one pair very small and oval-shaped; and one pair fairly large, straight, and rod-shaped. The first three pairs are called *autosomes*, and the last pair sex or X chromosomes (see Fig. 75). The chromosomal make-up of males is similar to that of females regarding the autosomes but the male has an odd pair, one of the pair being an X chromosome, like that found in the duplicate in the female, the other member of the pair being somewhat smaller, with a hook or bent portion at one end, and called the Y chromosome.

XY Type of Sex Inheritance.—In the breeding work with Drosophila, which normally have red eyes, a white-eyed mutant male was found by Morgan. This male was saved and, when mated to red-eyed females, yielded an F_1 all of which were red-eyed. The F_2 gave the expected 3 red:1 white phenotypic ratio but it was noted that the white-eyed

individuals were all males. This exception to usual Mendelian expectancy was finally explained by locating the gene for white eyes in the X chromosome. The F_1 female from a red-female white-male cross would therefore have two chromosomes, in one of which would be found the gene for red eyes, with the gene for white eyes in the other sex chromosome. Mated to a red-eyed male, she in turn would yield an F_2 with both of the females red-eyed, one male red-eyed, and the other white-eyed. The following diagram illustrates this cross.

White-eyed male sperms	Red-eyed female eggs		
	*R*X	*R*X	
*r*X	*R*X*r*X	*R*X*r*X	F_1 red-eyed females, heterozygous
Y	*R*XY	*R*XY	F_1 red-eyed males

and the F_2 produced by mating two F_1's

Red-eyed male sperms	Red-eyed female (heterozygous) eggs		
	*R*X	*r*X	
*R*X	*R*X *R*X	*R*X *r*X	F_2 red-eyed females, 1 heterozygous
Y	*R*XY	*r*XY	F_2 males, 1 red-eyed, 1 white-eyed

FIG. 85.—Checkerboard diagram of cross of red-eyed female and white-eyed male through F_2.

This is an example of sex-linked inheritance. It is seen that the female produces eggs, following reduction, all of which are alike as far as the sex chromosome is concerned, whereas the male produces two sorts of sperm cells in equal numbers, one containing an X chromosome and the other a Y chromosome. The sex of the offspring depends, therefore, on the type of spermatozoon that happens to fertilize the egg, an X egg plus an X-containing sperm yielding a female and an X egg plus a Y-containing sperm yielding a male. All characteristics that are determined by genes carried in the X chromosomes will, therefore, show this peculiar type of sex-linked inheritance. Many such characteristics have been discovered and catalogued.

Sex-linked Factors in Drosophila.—There is abundant substantiating proof of this theory from the behavior of sex-linked factors. The sex chromosomes (chromosome I in the chart, Fig. 95) carry factors that determine characteristics just as do the other chromosomes. About 200 sex-linked characters have been discovered in the fruit fly. The factor for white eyes in Drosophila, for instance, is sex-linked. When

a white-eyed male *r*XY is mated to a red-eyed female *R*X*R*X, the F_1 offspring all have red eyes, because red eye is dominant to white eye in Drosophila. In the F_2, red- and white-eyed flies are produced in the proportion of 3 red:1 white. All the females of this generation are red-eyed, but of the males ½ have red eyes and ½ have white eyes. When the reciprocal cross is made, *i.e.*, when a white-eyed female is mated to a red-eyed male, the results are different. In the F_1 of such a mating, all the female flies have red eyes and all the male flies have white eyes. In the F_2 of this cross, ½ the females have red eyes and ½ have white eyes, and likewise among the males ½ have red eyes and ½ have white eyes.

	*r*X	Y
*R*X	*R*X*r*X	*R*XY
*R*X	*R*X*r*X	*R*XY

F_1 cross, white-eyed male and red-eyed female

↓

	*R*X	*Y*
*R*X	*R*X*R*X	*R*XY
*r*X	*R*X*r*X	*r*XY

F_2 cross, white-eyed male and red-eyed female

	*R*X	Y
*r*X	*R*X*r*X	*r*XY
*r*X	*R*X*r*X	*r*XY

F_1 cross, red-eyed male and white-eyed female

↓

	*r*X	Y
*R*X	*R*X*r*X	*R*XY
*r*X	*r*X*r*X	*r*XY

F_2 cross, red-eyed male and white-eyed female

Fig. 86.—Diagram of cross of white-eyed male × red-eyed female and the reciprocal.

In the foregoing diagrams the presence of two X chromosomes determines a female, an X and a Y chromosome determine a male. The presence of at least one *R* determines red eyes, because red eye is dominant to white. It has been pointed out previously that, aside from the pair of sex chromosomes, the pairs of chromosomes in both the male and the female of Drosophila are alike and carry corresponding factors or determiners of characteristics. In this type of sex inheritance, the female is homogametic for the sex chromosome. A variation of the XY type of sex determination occurs in some species that lack the Y chromosome. Here the females are XX but the males are XO (Y chromosome lacking). It is evident, however, that the male will still produce two types of spermatozoa, one containing an X chromosome, the other lacking an X chromosome.

Sex-linked Characters in Man.—In the human family a sex-linked characteristic is that of color blindness, or the inability, through an inherent defect in the eye, to distinguish between various colors. It is well known that there are many more color-blind men than women, the

reason for which should soon be evident. Representing normal vision with *C* and color blindness with *c*, the following is the genetic make-up of a normal visioned woman *CXCX* and of a color-blind man *cXY*. Such mating would give children in the F_1 all of whom would be normal-visioned, though all the daughters would be carriers of color blindness. In the F_2, there would be 3 normal-visioned children (2 daughters and 1 son) to 1 color-blind child (son). The reciprocal cross is also diagrammed as shown in Fig. 87.

	*c*X	Y
*C*X	*C*X*c*X	*C*XY
*C*X	*C*X*c*X	*C*XY

F_1 cross, color-blind man and normal-visioned-woman

	*C*X	Y
*c*X	*C*X*c*X	*c*XY
*c*X	*C*X*c*X	*c*XY

F_1 cross, normal-visioned man and color-blind woman

	*C*X	Y
*C*X	*C*X*C*X	*C*XY
*c*X	*C*X*c*X	cXY

F_2 cross, color-blind man and normal-visioned woman

	*c*X	Y
*C*X	*C*X*c*X	*C*XY
cX	cX*c*X	cXY

F_2 cross, normal-visioned man and color-blind woman

FIG. 87.—Diagram of cross of color-blind man and normal-visioned woman and its reciprocal.

In the foregoing, two X chromosomes determine a female, an X and a Y chromosome determine a male, and at least one *C* determines the ability to differentiate colors. The occurrence of color-blind men is to be expected more frequently than color-blind women, for a double dose of the color-blind gene is necessary to produce a color-blind woman (*e.g.*, if 6 per cent of males were color-blind, then we could expect 0.06×0.06 or approximately 4 per cent of women to be color-blind).

WZ Type of Sex Inheritance.—Another type of sex inheritance, which, to distinguish it from the XY type, is called the WZ type, is found in poultry. Here the distinguishing feature is the fact that the male is homogametic for the sex chromosome, whereas the female is heterogametic. According to Castle, this condition is found in moths and in certain fish and birds; *e.g.*, in domestic fowls, pigeons, ducks, and canaries.

A well-known example of sex-linked inheritance in poultry is that of coat pattern. For instance, if a Plymouth Rock (barred) cock is mated to a black (or any other nonbarred breed), the F_1 offspring, both male and female, are barred. When these F_1 hybrids are mated, producing the F_2 generation, there results 3 barred individuals (2 males and 1 female) to 1 nonbarred or black (female). When the reciprocal cross is made, *viz.*, black cock mated to barred hens, there are produced in the

F_1 barred males and nonbarred, or black, females. When these F_1 hybrids are mated, producing the F_2 generation, ½ the number of males so produced are barred and ½ are black, and of the females ½ are barred and ½ are black. Diagrammatically, we have *B*, barred; *b*, black; ZZ, male; ZW, female.

	*B*Z	*B*Z
*b*Z	*B*Z*b*Z	*B*Z*b*Z
W	*B*ZW	*B*ZW

F_1 cross, barred cock and black hen

	*b*Z	*b*Z
*B*Z	*B*Z*b*Z	*B*Z*b*Z
W	*b*ZW	*b*ZW

F_1 cross, black cock and barred hen

	*B*Z	*b*Z
*B*Z	*B*Z*B*Z	*B*Z*b*Z
W	*B*ZW	*b*ZW

F_2 cross, barred cock and black hen

	*B*Z	*b*Z
*b*Z	*B*Z*b*Z	*b*Z*b*Z
W	*B*ZW	*b*ZW

F_2 cross, black cock and barred hen

FIG. 88.—Diagram of cross of barred cock and black hen and its reciprocal in F_2.

In the foregoing, two Z's determine a male, one Z and one W a female, and at least one *B* a barred individual.

In neither the XY nor the ZW type does crossing over take place in the individuals that are heterogametic for the sex chromosome. In some species the Y or W chromosome is lacking, giving XO or ZO types of spermatozoa or ova.

Sex-influenced Inheritance.—This type of inheritance is not to be confused with sex-linked inheritance, which has been discussed in the previous sections. In sex-linked inheritance the genes determining the characteristic are located in the X chromosome. Such is *not* the case in sex-influenced characters, the genes for such characteristics being located in the autosomes, *not* in the sex chromosomes.

Basically all characteristics are dependent on genes, or the interaction of genes plus, of course, a suitable environment, both external and internal. The environment, be it noted, is just as important as the genes. A cow, for instance, might have inherited the genes that would allow her to produce 10,000 lb. of milk under good environmental conditions, but, if she calves out in the woods and runs wild therein, it is doubtful whether she would give more than a few hundred pounds of milk.

Animals also have an internal environment, their own bodies, and it is apparently this internal environment that, together with genes, is the determining factor in the expression of sex-influenced characteristics. Both the male and the female are supplied with several sets of glands that secrete chemical substances which are picked up by the blood stream

and carried to all parts of the body, where they make their presence known through influencing the activities of cells in various parts of the body. These are known as the *endocrine*, or *ductless*, glands, and their secretions as *hormones*. The thyroid gland, which lies athwart the Adam's apple, secretes thyroxin, which plays a very important part in both physical and mental growth. The suprarenal capsules, situated just above the kidneys, secrete adrenalin, which helps to regulate the amount of sugar in the blood. The most important of these ductless glands is probably the pituitary gland, which lies embedded in a little bony socket at the base of the brain and is known to secrete a dozen or more hormones, among others those which incite and regulate sexual manifestations as well as lactation. The gross picture, as far as the above endocrines are concerned, is the same for both male and female.

However, the female has ovaries and the male testes, and, as noted in Chap. VI, these glands have an endocrine as well as a spermatogenetic or ovogenetic function. In other words, the internal environment of males and females is basically different, and herein lies the explanation of the expression of these so-called "sex-influenced" characteristics. In sheep, for instance, some breeds have horns in both sexes, some horns in the males only, and still other breeds are hornless in both sexes. If we crossed a horned breed (*hh*) with a hornless one (*HH*), the F_1 males will be horned (*Hh*) and the F_1 females (*Hh*) hornless. If we go on and get the F_2 from this cross, we find that among the males there is a ratio of 3 horned : 1 hornless, among the females a ratio of 3 hornless : 1 horned. Clearly the internal environment is influencing the expression of this characteristic. Warwick and Dunkle[1] have shown that genes *H* (hornlessness), *H'* (Dorset horns, *i.e.*, in both sexes) and *h* (Merino and Rambouillet horns, *i.e.*, horns in male, knobs in female) form a series of multiple alleles.

A somewhat similar situation is found regarding the inheritance of the very dark red (mahogany) color in Ayrshire cattle, the *Mm* genotype producing mahogany and white pattern in males, but red and white in females. In man, a certain type of baldness shows the same sort of inheritance.

Male		Female
mahogany and white	*MM*	mahogany and white
mahogany and white	*Mm*	red and white
red and white	*mm*	red and white

Still another sort of sex-influenced inheritance is that relating to cock and hen feathering in poultry. As is well-known, the differences in the plumage patterns between males and females are due to testicular and ovarian hormones. If the ovary of a bird belonging to a race that normally exhibits differences in male and female plumage is removed and

[1] See *Jour. Heredity*, **30**: 8, pp. 325–329.

a piece of testes transplanted into her, she will then proceed to develop the male feather pattern. A dominant gene (H) for hen feathering is known in poultry. Hens of whatever genetic constitution (HH), (Hh), or (hh) will be hen-feathered because they lack the proper internal environment, specifically the male sex hormone, to produce cock feathering. In males, the gene H prevents the development of cock feathering so that HH and Hh males are hen-feathered, whereas hh males are cock-feathered. The characteristic is therefore seen to be sex-limited to the male and to be due to the interactions of genes with the internal environment of the animal.

Probability.—Mathematics is coming to play a greater and greater part in genetic research owing to the fact that inheritance is traceable to particulate elements, genes, which, although functioning through a complex system of reproductive physiology, yet behave in an orderly, specific, predictable manner. Mendel's early success in discovering the basic laws of inheritance was due largely to the fact that he kept accurate records of the appearance of characteristics by separate generations and found that they followed a certain statistical regularity.

If we toss a penny, it has an even chance of falling heads or tails, the chance of its falling either being $\frac{1}{2}$. If we toss two pennies, the chance that one of them will fall heads is $\frac{1}{2}$, the chance that the other will fall heads is $\frac{1}{2}$, and the chance that both will fall heads is the product of the likelihood of each separate event or $\frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$. The same situation prevails for the likelihood of both falling tails. The chance that one will fall heads and the other tails is $\frac{1}{2} \times \frac{1}{2}$ or $\frac{1}{4}$, or that the former will fall tails and the latter heads is $\frac{1}{2} \times \frac{1}{2}$ or $\frac{1}{4}$, so that the chance of getting one head and one tail simultaneously is $\frac{1}{4} + \frac{1}{4}$ or $\frac{1}{2}$. Likewise if we toss three pennies we may get all heads, in fact, the chance that we will is definitely known to be $\frac{1}{2} \times \frac{1}{2} \times \frac{1}{2}$ or 1 chance in 8, and the chance that we will get two heads and one tail is again the product of the separate probabilities; *i.e.*, two heads $= \frac{1}{2} \times \frac{1}{2}$ or $\frac{1}{4} \times$ one tail $= \frac{1}{2}$ or $\frac{1}{8} \times 3 = \frac{3}{8}$, because with three coins being tossed the two-heads-and-one-tail combination can appear from any of three combinations. Likewise, we would have a $\frac{3}{8}$ chance of getting one head and two tails and a $\frac{1}{8}$ chance of getting three tails.

This is seen to be simply an expansion of the bionomial $(a + b)^n$, where $a = \frac{1}{2}$ and $b = \frac{1}{2}$ and n is any number. We can let a represent heads (chance $\frac{1}{2}$) and b represent tails (chance $\frac{1}{2}$). Therefore, we can quickly find the answer to the question, "How many times in tosses of three coins simultaneously will we get two heads and one tail? Expanding the bionomial we have $a^3 + 3a^2b + 3ab^2 + b^3$. Since we are dealing with the two heads and one tail combination and a stands for heads and b for tails, we select the second term of the expansion $3a^2b$ and substitute

the values for a, $(\frac{1}{2})$ and for b, $(\frac{1}{2})$ and we have $3 \times (\frac{1}{2})^2 \times \frac{1}{2}$ or $3 \times \frac{1}{4} \times \frac{1}{2} = \frac{3}{8}$.

The procedure is the same for any problem involving probabilities; *viz.*, first find the probability of each separate event and then substitute these values in the proper term of the expanded bionomial. If, for instance, we wanted to know how many times in clutches of 8 eggs from birds that are heterozygous for both A and B, *i.e.*, of the genetic constitution $Aa\ Bb$, we would get 6 feather-shanked and 2 clean-shanked birds, first, we must remember that these are duplicate factors and that either A or B or both will produce feathered shanks, while $aa\ bb$ is clean-shanked. The ratio from these parents is then 15 feathered : 1 clean. We will let a stand for feathered and b for clean. Now our term in the bionomial expanded to the eighth power is $a^8 + 8a^7b + 28a^6b^2$, and we now substitute the values for a and b, giving $28\left(\frac{15}{16}\right)^6\left(\frac{1}{16}\right)^2 = \frac{318,937,500}{4,294,966,296}$, or roughly $\frac{1}{13}$. In other words, once out of 13 times we can expect to get 6 feathered and 2 clean-shanked birds from clutches of 8 eggs when the parents are double heterozygotes for the two pairs of genes that act in a duplicate fashion in producing this characteristic.

In cases where there are three possibilities, *e.g.*, in a cross between two red hogs that are double heterozygotes for the two pairs of genes either dominant of which by itself produces sandy-colored hogs in a 9:6:1 ratio, we would have to expand the trinomial $(a + b + c)^n$.

In all cases the chromosomes assort and recombine at random according to the laws of probability.

Gene Manifestations.—Genes are the genetic representatives of specific characteristics. The exact nature of the physicochemical make-up of the genes is unknown. At present, they are known simply by their actions. It is the purpose here to point out some of the ways in which factors manifest themselves.

The simplest gene manifestation is of the sort where apparently one gene conditions the development of a certain characteristic, *e.g.*, the factor P, which brings about polledness in cattle. As a contrast to this may be considered the function of milk production, which is no doubt dependent on a great many genes, for milk production is a complex physiological phenomenon dependent among other things on the capacity, temperament, and vitality of the cow. One gene may have a very pronounced effect on the individual; *e.g.*, in peas, the gene T, which brings about tallness, whereas genes tt bring about dwarfness; or the gene may cause the early death of the individual (lethal genes). On the other hand, the gene may condition the development of a minor characteristic, such as eye color. The white eye in Drosophila, however, is only one of the several characters that such mutants exhibit, some of the others

being a lowered fertility and vitality; thus, one gene apparently affects many characteristics. The individuals of certain races may exhibit a good deal of variability, but the evidence would seem to point not to the unstable nature of the gene but rather to environmental effects as the source of this variability.

Entirely different genes may also bring about the identical characteristic in the organism.

We find, in experience, that we cannot safely infer from the appearance of the character what gene is producing it. There are at least three white races of fowls, produced by different genes. We can synthesize white-eyed flies that are somatically indistinguishable from the ordinary white-eyed race, yet they are the combined product of several known color-producing genes. The purple eye color of Drosophila is practically indistinguishable from the eye colors maroon and garnet.[1]

It should be emphasized that determiners are not characteristics. An animal does not inherit characteristics from its ancestors, but rather it does inherit potentialities. Whether the potentiality develops to its fullest extent in the animal depends upon the environment, and the term *environment* is here used in its widest sense. The new organism has an environment from the minute the egg is fertilized by the sperm; or we might go even further back and consider that the egg and sperm each has an environment before fertilization has been accomplished. The point is that the environment, speaking generally, may inhibit the full expression of potentialities from a time preceding fertilization until physiological maturity has been attained. Developmental aberrations in utero may affect the embryo deleteriously from either an anatomical or a physiological standpoint; and the same is true of a multitude of environmental conditions following birth. For example, even though an animal inherited the potentiality for large body size or high milk production, the end results actually obtained are capable of extensive modification through feeding and management. Likewise many people inherit the potentiality for having considerable pigment in their skin, but this is conditioned by the action of sunlight. In other words, we tan in summer and bleach in winter.

The Gene.—Up to the present, genes are known only indirectly; *i.e.*, we know them by their actions. That they are chemical structures of some sort is, of course, a generally accepted opinion. Mendel postulated some sort of entities within the germ cells that were held responsible for the appearance of certain somatic characters. Later genetic studies substantiated this idea, and the genes for many characters have been definitely located in certain chromosomes in relation to other genes in the

[1] Morgan, T. H., "Physical Basis of Heredity," pp. 239–240, J. B. Lippincott Company, Philadelphia, 1919.

same chromosome on the basis of their behavior in hereditary transmission. In brief, the gene is thought of as an organic unit, located in a definite place in the chromosome, which is in some manner capable of reproducing itself, and the genes in turn are held to be the responsible agents in making possible the appearance of all the characteristics of a new organism.

Various estimates have been made regarding the size of the gene, ranging from 10 to 70 mμ as the upper limit. In any event they must be exceedingly minute. Because of the fixed wave length of visible light, the smallest objects that can be seen distinctly with the highest powers of the microscope[1] are of the order of 250 mμ, *i.e.*, about 1/100,000 in. (1/100,000 in. compares with 1 in. as 1 in. compares with 1.58 miles.) By use of the ultraviolet light with its shorter wave length, objects of the order of 100 mμ have been photographed. Ordinary bacteria, without distinguishable nuclei or chromosomes but presumably containing genes, are of the order of 500 to 750 mμ, and the filterable viruses are thought to be of the order of about 10 to 250 mμ.

Summary.—In this chapter we have considered several additional types of inheritance. We have learned that there may be more than two alternative forms of a gene making manifest the principle of multiple alleles. We also have seen that many of the commercially valuable characters of our animals are determined by the interactions of a great many pairs of genes. It is this feature, plus the fact that our larger animals have so few offspring, that makes animal breeding so difficult. We have also become acquainted with the action of lethal genes as well as the various types of inheritance associated with or dependent upon the sex of the individuals. Finally, we have seen that the transmission of potentialities from ancestors to offspring behaves in an orderly fashion which is predictable on the basis of the laws of chance or probability, that the final result of gene action may follow a variety of patterns, and that cytology is working ever closer to a satisfactory explanation of the nature of the basis of all living matter, the gene.

References[2]

Problems

1. If two chinchilla rabbits produce both chinchilla and albino offspring, what are the genotypes of all these animals?

2. Could two chinchilla rabbits produce both Himalayan and albino offspring?

3. What are the genotypes of the parents in the following rabbit crosses:

(*a*) Colored × colored give 3 colored and 1 albino.

(*b*) Colored × chinchilla give ½ colored; ¼ chinchilla; ¼ Himalayan.

[1] The current development of the electron microscope may soon permit much more detailed physical knowledge of the chromosomes and genes.

[2] See lists at end of Chaps. XII and XIII.

(*c*) Chinchilla × Himalayan give ½ chinchilla; ½ Himalayan.
(*d*) Colored × Himalayan give ½ colored; ½ Himalayan.
(*e*) Chinchilla × Himalayan give ½ chinchilla; ¼ Himalayan; ¼ albino.

4. What will be the phenotype, as to blood groups, of offspring of parents of the following genotypes for blood groups:

$$Aa \times a^b a$$
$$Aa^b \times a^b a$$
$$a^b a \times a^b a$$

5. If a person of blood group *AB* marries one belonging to group *O*, what will be the blood groups of their children?

6. NOTE.—In the three following problems on blood groups, determine the genotypes of the parents.

One parent is group *A* and the other group *B*, but all four groups are represented among the children.

7. Both parents are group *A*, but ¾ of the children belong to group *A* and ¼ to group *O*.

8. One parent is *AB* and the other *B*, but of the children ¼ are *A*, ¼ *AB*, and ½ *B*.

9. In the two following cases of disputed paternity, determine the true father of the child: (*a*) The mother belongs to group *B*, the child to *O*, one possible father to *A* and the other to *AB*. (*b*) the mother belongs to group *B*, the child to *AB*, one possible father to *A* and the other to *B*.

10. In the choice of donors for blood transfusion, a patient's brother or sister is often selected. Would these be more likely to be successful donors if both parents belonged to blood group *AB* or if both belonged to group *O*? Explain.

11. If both parents belong to blood group *AB*, what proportion of their children would be expected to be of such a type as to be able to give blood to their parents?

12. Consult the chromosome map for Drosophila (p. 357) and determine how many dominant genes must be present in each chromosome to give the normal red eye color.

13. If a rose-combed creeper male is mated to rose-combed creeper female and produces some single-combed normal birds, what were the genotypes of the parents?

14. NOTE.—In poultry, creeper is a semidominant lethal, barring a sex-linked dominant.

A cross of creeper, barred female and normal, nonbarred male would give what offspring?

15. A cross of creeper, heterozygous barred male and creeper, nonbarred female would give what offspring?

16. A cross of creeper, double-heterozygous walnut-combed, barred female and normal, rose-combed, heterozygous barred male would give what offspring?

17.* A sex-linked recessive lethal factor is known in poultry. What would be the sex ratio of the offspring of a male, heterozygous for the lethal, crossed with normal females?

18.* In a certain series of matings between normal pigs, 38 offspring were born. Of these 29 were normal, and 9 had greatly swollen forelegs. The latter lived only a few hours. How could these results be explained genetically?

19.* In the Tzourcana sheep of Roumania, gray individuals and black individuals are found. The black animals when bred together give all black offspring. Black

* NOTE.—In this list the problems that are starred are taken from Snyder, "Principles of Heredity," D. C. Heath and Company, Boston, 1940, and are reproduced here through the kind permission of the author and publishers.

mated to gray results in approximately equal ratios of black and gray lambs. When grays are mated together, approximately two thirds of the offspring are gray, and one third black. What kind of inheritance appears to be involved?

20.* In a certain strain of Oldenburger horses, tracing back to the mare, Jelka, the females of the line regularly produce only half as many male offspring as female offspring. What genetic explanation can you suggest for this?

21.* In cattle, the polled condition is dependent upon a dominant factor (P), the horned condition upon its recessive allele (p). In the Dexter-Kerry cattle the short-legged (Dexter) condition is dependent upon a dominant lethal factor (D), the long-legged (Kerry) condition upon its recessive allele (d). Suppose a Dexter bull homozygous for polled were mated to a horned Dexter cow. What kinds of calves could they produce, and in what proportions?

22.* Suppose two polled Dexter animals were mated and produced a horned Kerry calf. What would be the genotypes of the parents?

23.* What kinds of offspring would be expected from the mating of two horned Kerry animals? Two horned Dexter animals?

24. NOTE.—Assume that in man the difference in skin color between negro and white is due to two pairs of factors; that *AA BB* is "black" and ***aa bb*** "white"; and that any three of these factors produce "dark" skin; any two, "medium"; and any one "light."

What will be the skin color of the offspring from a mating of white with black? From a mating of two individuals genotypically like these F_1 offspring?

25. What are the genotypes of the parents in the two following matings of negroes: medium × light, giving ⅛ dark, ⅜ medium, ⅜ light, ⅛ white; medium × light, giving ½ medium and ½ light?

26.* A variety of squash bearing six-pound fruits is crossed with one bearing three-pound fruits. The F_1 plants bear four-and-a-half-pound fruits. Among the F_2 fruits there is considerable variation, but out of 200 such fruits there are three which weigh as little as three pounds, and three which weigh six pounds. How many pairs of factors are responsible for the difference in weight between the two parent lines, and how much does each effective allele contribute to this difference?

27.* How many different homozygous strains bearing four-pound fruits could be developed?

28.* A race of oats yielding 10 grams per plant was crossed with a race yielding 4 grams per plant. The F_1 plants yielded 7 grams per plant. Out of 253 F_2 plants, four yielded as much as 10 grams per plant and four yielded as little as 4 grams per plant. How is yield inherited in these oats?

29.* In the preceding problem, how much does each effective allele contribute to yield?

30.* Two different races of corn each averaging 68 inches in height were crossed. The F_1 also averaged 68 inches in height. In the F_2, however, there was considerable variation, ranging from 36 inches to 100 inches. Out of 1,942 F_2 plants, eight reached a height of 100 inches, and seven were as short as 36 inches. Explain these results in terms of genetic factors, assuming that the environment was held similar for these plants.

NOTE.—Color blindness and hemophilia in man are sex-linked recessives.

31. A girl of normal vision whose father was color-blind marries a man of normal vision whose father was also color-blind. What types of vision will be expected in their offspring?

32. A color-blind man marries a woman of normal vision. They have sons and daughters, all of normal vision and all of whom marry normal persons. Where among the grandchildren may color blindness be expected to appear? If there are cousin

marriages among these grandchildren, where among their offspring may color blindness be expected to appear?

33. A man and woman, both of normal vision have (*a*) a color-blind son who has 1 daughter of normal vision: (*b*) a daughter of normal vision who has 1 color-blind and 1 normal son; and (*c*) another daughter of normal vision who has 5 sons, all normal. What are the probable genotypes of grandparents, children, and grandchildren?

34. A brown-eyed woman with normal vision whose father was color-blind and blue-eyed marries a man who is blue-eyed and of normal vision. What offspring may this couple expect as to eye color and vision?

35. A man (A) with hemophilia marries a normal woman (B). Their daughter (C) marries a man (D) with hemophilia and produces 2 sons, 1 (E) with hemophilia. The normal son (F) marries a woman (G) whose paternal grandfather (H) has hemophilia but whose parents (I and J) were apparently normal. What are the genotypes of all the individuals concerned?

36. A man's maternal grandmother had normal vision; his maternal grandfather was color-blind; his mother is color-blind; his father is of normal vision. What are the genotypes, as to vision, of the two parents and grandparents mentioned? What type of vision has this man himself? What type have his sisters? If he should marry a woman genotypically like one of his sisters, what type of vision would be expected in the offspring?

37. The mother of a right-handed brown-eyed woman of normal vision is right-handed, blue-eyed, and of normal vision, and her father is left-handed, brown-eyed, and color-blind. This woman marries a man who is left-handed, brown-eyed, and of normal vision whose father was blue-eyed. What chance will the sons of this couple have of resembling their father phenotypically?

38. What effect on the sex ratio would a recessive sex-linked lethal factor have in man?

NOTE.—Barred plumage in poultry is a sex-linked dominant.

39. In poultry, if a nonbarred cock is crossed with a barred hen, and an F_1 female from this cross is mated with her father and an F_1 male with his mother, what will be the appearance of the offspring of these last two crosses, as to barring?

40. A single-combed barred cock crossed with a walnut-combed barred hen produces the following offspring:

4 rose, barred males.
5 walnut, barred males.
2 rose, barred females.
3 rose, nonbarred females.
2 walnut, barred females.
2 walnut, nonbarred females.

What are the genotypes of the parents?

41. In poultry, assume high egg laying to be determined by two factors, one of which, *M*, is sex-linked and the other, *L*, not sex-linked. A breeder has two high-producing hens and five males of unknown genotypes. Each hen is bred to each male with results as follows:

Hen 1 × male 1 gives 3/8 high, 1/2 medium, and 1/8 low layers.
Hen 1 × male 2 gives 1/4 high, 1/2 medium, and 1/4 low.
Hen 1 × male 3 gives 1/2 high, 1/2 medium.
Hen 1 × male 4 gives 3/4 medium, 1/4 low.
Hen 1 × male 5 gives 1/2 medium, 1/2 low.

Hen 2 × male 1 gives ½ high, ½ medium.
Hen 2 × male 2 gives ½ high, ½ medium.
Hen 2 × male 3 gives ½ high, ½ medium.
Hen 2 × male 4 gives all medium.
Hen 2 × male 5 gives all medium.

What are the probable genotypes for fecundity of these seven birds?

From which of these ten crosses would you be most likely to get the best males for producing high-laying hens?

42. NOTE.—White eye in Drosophila is a sex-linked recessive.

In Drosophila, if a white-eyed female is crossed with a red-eyed male and the F_2 allowed to interbreed freely, what will be the appearance of the F_3 as to eye color?

43. In Drosophila, if a homozygous red-eyed female is crossed with a white-eyed male and the F_2 allowed to interbreed freely, what will be the appearance of the F_3 as to eye color?

44. In Drosophila, vestigial wings (v) are recessive to the normal long wings (V), and the gene for this trait is not in the sex chromosome. If a homozygous white, long female is crossed with a homozygous red, vestigial male, what will be the appearance of the F_1? Of the F_2? Of the offspring of a cross of the F_1 with each parent type?

45. In Drosophila, two red-eyed long-winged flies when bred together produce the following offspring: females, ¾ red, long; ¼ red, vestigial; males, ⅜ red, long; ⅜ white, long; ⅛ red; vestigial; ⅛ white, vestigial.

What are the genotypes of the parents?

46. In Drosophila, a cross between bar-eyed female and wild-type (round-eyed) produces only bar-eyed male and female in the F_1. Wild-type female crossed with bar-eyed male produces bar female and wild-type male. Explain the inheritance of bar eyes and predict the appearance of the F_2 from each of these crosses.

47. If a white-eyed nondisjunctional female Drosophila, $(Xr)(Xr)Y$, is mated to a red-eyed male, what kinds of offspring may be expected as to sex and eye color?

48. A factor l in Drosophila is recessive, lethal, and sex-linked. If female Ll is crossed with a normal male, what should be the sex ratio of the progeny?

49. In Drosophila vermilion eye color is recessive and sex-linked. In exceptional cases vermilion female crossed with normal male produces, in addition to the usual vermilion male and red-eyed female, a few vermilion female and red male. Explain this result and predict what classes of offspring should appear when the vermilion F_1 females from above are crossed with red-eyed males.

50. In Drosophila yellow body color (y) is sex-linked and recessive to the gray (Y) body of the wild fly.

If a yellow female is crossed with a gray male, and (a) if an F_1 female from this cross is mated with her father and (b) an F_1 male mated with his mother, what will be the appearance of the offspring of these last two crosses as to body color?

51. If a hen that undergoes sex reversal, and thus becomes a functional male, produces gametes of the same chromosomal constitution as before (although they are now sperms instead of eggs), what will be the sex of her offspring when she is mated with a normal hen?

52. If such a sex-reversed hen were barred, what would be the appearance of her offspring when bred to a nonbarred hen?

53.* A bald man whose father was not bald marries a non-bald woman whose mother was bald. What are the genotypes of these two people in regard to the factors for baldness and non-baldness? What kinds of children can they have in regard to these characters?

54.* A non-bald, normal-visioned man marries a non-bald, normal-visioned woman whose father was color-blind and whose mother was bald. What kinds of offspring may they have, and in what proportions?

55.* A non-bald man marries a non-bald woman. They have a son and a daughter. At the age of thirty-five the son becomes bald. What are the chances that the daughter will also become bald because of her genetic constitution?

56.* A red-and-white Ayrshire cow whose mother was mahogany-and-white is bred to a red-and-white Ayrshire bull. If she produces a male calf, what are the chances that it will be mahogany-and-white? If the calf is a female, what are the chances that it will be mahogany-and white? This is a sex-influenced character.

57.* Outline the breeding procedure necessary to establish a homozygous mahogany-and-white Ayrshire herd.

58.* Outline the breeding procedure necessary to establish a homozygous red-and-white Ayrshire herd.

59. NOTE.—In sheep, white fleece (W) is dominant over black (w); and the horned condition (h) is dominant over the hornless (H) in males but recessive in females.

If a homozygous horned, white ram is bred to a homozygous hornless, black ewe, what will be the appearance of the F_1 and the F_2 as to color and horns?

60. A horned, black ram bred to a hornless, white ewe has the following offspring: Of the males, ¼ are horned, white; ¼ horned, black; ¼ hornless, white; and ¼ hornless, black. Of the females, ½ are hornless, black and ½ hornless, white. What are the genotypes of the parents?

61.* How many times in families of five would you expect four boys and a girl? Four girls and a boy? Five girls?

62.* In a certain family there are six girls. What are the chances of the next child being a boy?

63.* In human beings, deaf-mutism may be the result of the homozygous state of either or both of two recessive factors d and e. Normal hearing results only when both dominants D and E are present. When both parents are $Dd\ Ee$, how many times in families of two would you expect two deaf children?

64.* Where both parents are $Dd\ Ee$, how many times in families of four would you expect three normal children and one deaf child?

65.* Two normal parents produce an albino son. What are the chances that their next child will be a normal girl?

66.* In Shorthorn cattle, the factors for red and white are alleles but neither is dominant, the heterozygous condition resulting in roan. Twins are sometimes born in cattle. If twins are born in crosses between red bulls and roan cows, how often should both twins be roan?

67.* In poultry, feathered shanks are the result of either or both of the dominant factors F and S. Unfeathered shanks are the result of the double recessive condition. In crosses where both parents are $Ff\ Ss$, how many times in families of three offspring would all be expected to have feathered shanks? All three unfeathered shanks?

68.* If one parent were $Ff\ Ss$ and the other $ff\ ss$, how many times in families of four offspring would you expect one feathered-shank bird and three unfeathered-shanked birds?

69.* In poultry, the factors for black and for splashed-white are alleles but neither is dominant, the heterozygous condition resulting in blue (the Blue Andalusian). A pair of Blue Andalusians are mated, and the female lays two eggs. What are the chances that both eggs will hatch out Blue Andalusians?

70.* If three eggs are laid by the bird mentioned in Prob. 69, what are the chances that all three eggs will hatch out Blue Andalusians?

CHAPTER XV

THE PRINCIPLES OF HEREDITY *(Continued)*

Thus far we have studied various types of inheritance that behave as if certain characters were dependent on one pair of genes. Sometimes these genes were in an autosomal chromosome, sometimes in a sex chromosome, sometimes the gene was a dominant or a recessive lethal, sometimes the manifestation of the character was influenced by the sex of the individual. We also discovered that the gene may have more than just two alternative forms, that there may be three or many more genes in a series of multiple alleles.

In addition, we have studied the behavior of two genes simultaneously, both in cases where each pair of genes was responsible for the production of a separate character and those in which the two pairs of genes acted on only one character. In the latter cases, we met many exceptions to the general dihybrid 9:3:3:1 ratio due to various types of epistasis, and we also learned that lack of dominance in one or both pairs of genes can change this ratio. If, however, each of two pairs of genes causes the development of a certain separate character, or in some cases (*e.g.*, comb pattern in poultry) both act on the same character, if there is dominance between the members of each pair of genes, and if the pairs of genes are located in different chromosomes, then the F_2 will give the usual 9:3:3:1 ratio. If instead of mating two F_1's (*Aa Bb*) to get the F_2 we made what is termed the *backcross* by mating an F_1 (*Aa Bb*) to the double recessive (*aa bb*), then we would get equal numbers of four different phenotypic types according to the following diagram.

F_1 (*Aa Bb*) germ cells	*AB*	*Ab*	*aB*	*ab*
Double-recessive (*aa bb*) germ cells *ab*	*Aa Bb*	*Aa bb*	*aa Bb*	*aa bb*

Because each chromosome consists of scores or hundreds of genes, it is logical to suppose that we might sometimes be dealing with two pairs of genes that are located in the same chromosome. In such a case the genes would not assort independently, although the chromosomes would. Genes located in the same chromosome show varying degrees of linkage.

Linkage.—In working with sweet peas in 1906, Bateson and Punnett made a cross involving purple flowers and long pollen grains in one parent

and red flowers and round pollen grains in the other. Because crosses of purple and red had given a 3:1 ratio in the F_2 (purple being dominant) and crosses of long and round pollen grains had likewise given a 3:1 ratio in the F_2 (long pollen grains being dominant), it was expected that the F_2 of the purple, long crossed with red, round cross would give a ratio of 9 purple, long:3 purple, round:3 red, long:1 red, round. Such, however, was not the case, for out of 6,952 F_2 flowers 4,381 (instead of the expected 3,910.5) were purple, long; 390 (instead of 1,303.5) were purple, round; 393 (instead of 1,303.5) were red, long; and 1,338 (instead of 434.5) were red, round. Combinations of the two genes that had gone into the hybrid together (purple and long from one parent and red and round from the other) were much too numerous in the F_2. Actually there was a total of 6,169 of these two classes where only 4,345 had been expected. Bateson and Punnett called this feature *coupling*, and its opposite, where a dominant and a recessive were supplied by each parent (purple and round and red and long) and still too few of the new types appeared in the F_2, *repulsion*, these of course being different aspects of the same problem.

Facts like these stood out as exceptions to Mendelian inheritance until 1910, when Morgan and his coworkers at Columbia University discovered the basis for these phenomena from their work with Drosophila and coined the term that describes them, *linkage*. If two genes with recognizable end products are in the same chromosome, they will, of course, have more or less tendency to be inherited together.

In Drosophila, if a cross between a wild-type (gray) body color with long wings and a black body color with vestigial wings is made, the F_1 all have gray bodies and long wings, for these patterns are dominant to black and vestigial. If a male of this F_1 hybrid generation is mated to a black, vestigial female, we would expect to get some gray, long; gray, vestigial; black, long; and black, vestigial offspring. If the genes for these characters were in different chromosomes, we would expect equal numbers of the above classes. If they were in the same chromosome, we would expect to get more than 50 per cent of the grandparental types and less than 50 per cent of the new combinations. Actually, in this case, we get 100 per cent of the grandparental types and 0 per cent of new combinations. In other words, these genes remain completely linked when tested by this backcross.

The backcross to the double recessive is used to determine the sort of germ cells that the F_1 dihybrid is producing, because there is nothing in the double recessive to hide what is going on in the dihybrid.

The usual system of notation when dealing with linkage problems is to use the plus sign for wild-type genes (usually dominant) and a letter for the mutated gene. In the above case, the notation applicable with

independently assorting genes, *e.g.*, *GG LL* for a gray-bodied long-winged fly cannot be used because we know from the genetic behavior that the genes for gray body and long wings are in the same chromosome and, therefore, belong together. We could write the genetic make-up of such a fly $(GL)(GL)$, but it is more convenient to write it $++/++$ (plus sign standing for the wild-type genes).

Thus a diagram of the above cross would be written

$$P_1 \frac{++}{++} \times \frac{gl}{gl}$$

gray, long   black, vestigial

$$F_1 \frac{++}{gl}$$

gray, long male

and the backcross of an F_1 male to the double recessive

$$\frac{++}{gl} \times \frac{gl}{gl} = \frac{++}{gl} \text{ and } \frac{gl}{gl}$$

gray, long 50%   black, vestigial 50%

Crossing Over.—We have just seen that the backcross of a dihybrid gray-bodied long-winged male, $++/gl$, to a double-recessive black, vestigial female, gl/gl, gives only two sorts of offspring, ½ of them being gray, long, $++/gl$, and ½ black, vestigial, gl/gl, because the linkage of the G and the L genes and the g and l genes in the dihybrid male was complete.

However, if we take a dihybrid female with gray body and long wings, $++/gl$, and mate her to a double-recessive male, gl/gl, we will secure four kinds of offspring instead of two, *viz.*, gray, long; black, vestigial; black, long; and gray, vestigial. The reason for this evidently is that there has been crossing over between the loci for body color and length of wings, as illustrated in Fig. 89. The end result is that the genes G and L and g and l in this female dihybrid usually stay together but occasionally through crossing over get into the new combinations of G and l and g and L, or $+l$ and $g+$.

The above schematic diagram shows the manner in which the new gene combinations are formed. We have learned earlier that the pairs of homologous chromosomes come to lie side by side during the early stages of germ-cell production in the process called *synapsis*. In the early stages of synapsis, each member of each homologous pair of chromosomes reproduces itself so that the pair of homologous chromosomes becomes two pairs of closely associated sister chromatids. Crossing over, or the equal interchange of blocks of genes in sections, apparently

takes place between two nonsister chromatids after the two chromosomes have become bundles of four chromatids. In other words, crossing over involves two chromatids rather than two chromosomes.

In mitosis, or somatic cell division, the chromosomes shorten and thicken and arrange themselves in the equatorial plate (prophase). They next split or reproduce themselves (metaphase) so that each chromosome is now double. The members of each exactly similar doublet now start to move to opposite poles of the cell (anaphase). Finally the migration is complete (telophase), and the cell wall constricts, forming two cells exactly like the parent cell. In other words, in mitosis the chromosomes appear in the diploid number of paired threads. In meiosis, or germ-cell production, however, they appear as the haploid number of paired threads. This latter feature is due to synapsis, or conjugation of the homologous chromosomes, which is specific in that all the allelic genes are attracted to each other and come to lie side by side in a regionally specific fashion—gene *A* with *A* or *a*, gene *B* with *B* or *b*, etc.

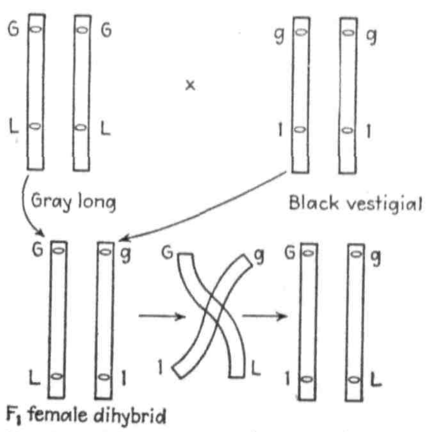


FIG. 89.—Schematic crossing over between loci for body color and wing length.

In the earliest prophase stage of meiosis, the chromosomes are strung out into long unpaired threads in the diploid number (leptotene stage). They next are attracted into homologous pairs (zygotene stage or synapsis). They next split or reproduce into bundles of four chromatids, two from each chromosome (pachytene stage). Finally in the last stages of prophase (diplotene, diakinesis) they show chiasma as the paired chromatids begin to open out. During these four stages the chromosomes have been shortening and thickening.

Each group of two sister chromatids is held together by an unstaining portion of the chromosome called a *centromere*. These centromeres appear to repel each other, and, as the bundle of four chromatids begins to be drawn apart by the retreating centromeres pulling each pair of two sister chromatids (formed from one chromosome) to opposite poles along the plane of conjugation, two of the nonsister chromatids often appear to be crossed, these crosses being chiasmata (singular, chiasma). These crosses are apparently due to one of a pair of sister chromatids breaking at the original point of the chiasma and becoming attached to the remaining portion of one of the members of the other pair of sister

chromatids and the remaining portions of the two broken chromatids themselves uniting into a whole chromatid as diagramed in Fig. 90.

It is obvious that, if crossing over took place in every cell containing the chromosomes diagramed in Fig. 90, the result would be equal numbers of *GL*, *Gl*, *gL*, and *gl* germ cells and would amount to 50 per cent of crossing over. Such a situation could not be differentiated genetically from independent assortment. Actually such a situation is not known. The greatest amount of crossing over yet found amounts to about 48 per cent, the least, 0 per cent as illustrated earlier in the Drosophila cross involving the use of a *GL*/*gl* male on *gl*/*gl* females, from which only *GL*/*gl* and *gl*/*gl* offspring resulted.

It has been found that the number of chiasmata at any given region is about twice the amount of crossing over. Again referring to Fig. 90,

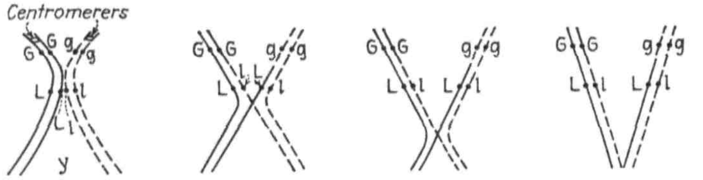


FIG. 90.—Diagram of chiasma at *x* with resulting crossing over between the genes *G* and *L*, thus resulting in the production of germ cells containing *GL*, *Gl*, *gL*, and *gl* genes.

if we were considering 100 sets of these chromosomes and found no chiasma in 80 of them, all of these resulting germ cells would contain the original combinations *GL* and *gl*. The other 20 per cent would show chiasma, but 25 per cent of the resulting germ cells would contain *GL* and 25 per cent *gl*, whereas the other 50 per cent (of the 20) would be *Gl* and *gL* (25 per cent of each). In other words, there were 20 per cent of chiasma to but 10 per cent of crossovers. Crossing over takes place between only two of the four chromatids, in something less than 100 per cent of the possible cases and always between two nonsister chromatids.

Crossover percentage, of course, is obtained by dividing the total number of crossovers by the total population. Morgan gives, among others, the following instances of crossing over in Drosophila:

When a black fly with vestigial wings is crossed to a wild-type ("gray") fly with long wings the offspring are, as we have already seen, gray, long. If one of the F_1 females is back-crossed to a black vestigial male there are four kinds of offspring produced; *viz.*, the two original combinations, black vestigial, and gray long; and in addition two recombinations of these; *viz.*, black long, and gray vestigial. The two latter classes are called the crossover classes, or, more briefly, crossovers. The percentage of crossovers is definite for a given stock, of a given age, and under given environmental conditions. In this case the percentages are as follows:

Non-crossovers		Crossovers	
Black vestigial	Gray long	Black long	Gray vestigial
41.5 per cent	41.5 per cent	8.5 per cent	8.5 per cent
83 per cent		17 per cent	

If a pair of chromosomes in the F_1 fly is represented as carrying the genes of the characters here involved, one member of such a pair carries both a gene for black and a gene for vestigial; the homologous member of the pair of chromosomes carries both of the normal alleles; *viz.*, a gene for gray and a gene for long wings. When crossing over takes place so that a gene for black goes over into the other chromosome, the converse phenomenon takes place, a gene for gray goes over into the chromosome that gave up its black gene. It is the constancy of this interchange that makes the phenomenon reducible to exact mechanical treatment.[1]

Using the usual notation, we would have, in this last cross of an F_1 female from a gray, long crossed with black, vestigial mated back to a double-recessive black, vestigial, the results indicated in the following diagram.

$$\frac{++}{++} \times \frac{gl}{gl}$$

gray, long ↘ ↙ black, vestigial

$$F_1, \frac{++}{gl} \text{ female} \times \frac{gl}{gl} = \text{backcross}$$

F_1 germ cells plus double-recessive germ cell,	$\frac{++}{gl}$	$\frac{gl}{gl}$	$\frac{g+}{gl}$	$\frac{+l}{gl}$
	gray, long	black, vestigial	black, long	gray, vestigial
numbers,	41.5%	41.5%	8.5%	8.5%
	noncrossovers		crossovers	

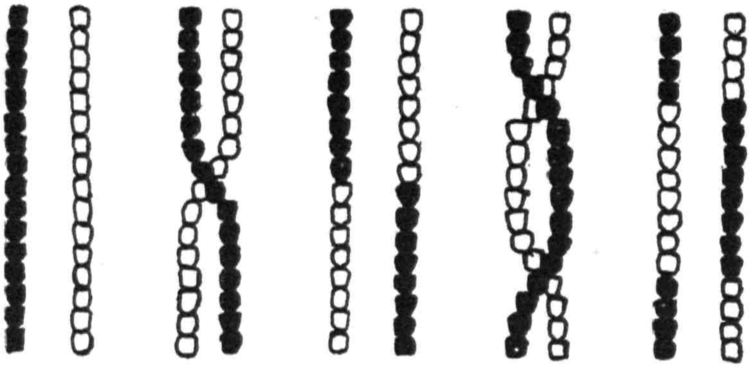
Strength of linkage = 83% Crossover percentage = 17%

The reduction in the number of chromosomes in the germ cells is accomplished by the two meiotic divisions. In the first, the chromosomes after synapsing become double through reproducing or splitting, each chromosome forming two chromatids closely applied to each other. This bundle of four chromatids then separates along the plane of conjugation (with possible crossing over), two closely applied sister chromatids passing to each secondary spermatocyte or oöcyte, this division being spoken of as the *heterotypic* division. These secondary germ cells then quickly go through another cell division, at which time one member of each pair of sister chromatids goes to each resulting cell. This is known as the *homotypic* division, and through these two rapid cell divisions the number of chromosomes is both reduced to one-half and the possibility of recombination of blocks of genes from the two parents provided.

It is readily seen in Fig. 90 that if another pair of genes C and c were located near the bottom of the chromosomes, and if another chiasma

[1] Morgan, T. H., "The Physical Basis of Heredity," pp. 87–88, J. B. Lippincott Company, Philadelphia, 1919.

appeared at point *y*, we might have a repetition of the above-described process with the result that genes *GlC* and *gLc* might be located in two chromatids. This would be a case of double crossing over, and, although two crossings over had occurred between *G* and *C*, they would still be in the same chromatid, which makes it appear genetically that no crossing over had occurred between them. Thus each case of double crossing



1 2 3 4 5

FIG. 91.—Diagrammatic representation of single crossing over between homologous chromosomes 1–3; and double crossing over 4 and 5.

over hides two actual crossovers, and allowance must be made for this fact in ascertaining crossover percentages involving situations of this sort.

If, in any cross involving genes located in the same chromosome and thus showing various degrees of linkage, the crossover percentage is

	4 *AB* (40%)	1 *Ab* (10%)	1 *aB* (10%)	4 *ab* (40%)
4 *AB* (40%)	16 (*AB*) (*AB*)	4 (*Ab*) (*AB*)	4 (*aB*) (*AB*)	16 (*ab*) (*AB*)
1 *Ab* (10%)	4 (*AB*) (*Ab*)	1 (*Ab*) (*Ab*)	1 (*aB*) (*Ab*)	4 (*ab*) (*Ab*)
1 *aB* (10%)	4 (*AB*) (*aB*)	1 (*Ab*) (*aB*)	1 (*aB*) (*aB*)	4 (*ab*) (*aB*)
4 *ab* (40%)	16 (*AB*) (*ab*)	4 (*Ab*) (*ab*)	4 (*aB*) (*ab*)	16 (*ab*) (*ab*)

FIG. 92.—Checkerboard showing the expected composition of the F_2 from a cross between individuals differing in two linked genes which show 20 per cent of crossing over. The F_2 ratio is 66 *AB*:9 *Ab*:9 *aB*:16 *ab*.

found to be 20 per cent, the same fact can be stated by saying that the strength of the linkage is 80 per cent.

Under standard conditions the percentage of crossing over remains constant between any two pairs of genes. However, experimental work has shown that a variety of internal and external conditions may affect this rate. Among these influences are sex, no crossing over in the male of Drosophila normally, although this can be induced in the autosomes by X-ray treatment; chromosomal aberrations such as the inversion of a section of the chromosome, translocations, etc., as well as gene mutations; and, in addition, age and temperatures.

Much of the study of crossing over is made by means of the back-cross. However, the F_2 is sometimes used and mathematical formulas have been devised for the interpretation of the results.

If we were dealing with a case that showed 20 per cent of crossing over between two genes *AB* and *ab*, then the F_2 ratios could be found by the usual checkerboard arrangements, as illustrated in Fig. 92.

Cytological Proof of Genetic Crossing Over.—We have looked at the evidence that crossing over takes place. We saw that a cross involving a gray-bodied long-winged female Drosophila of genetic constitution $++/gl$ and a double recessive male gl/gl gave four types of offspring, $++/gl$, gl/gl, $+l/gl$, and $g+/gl$, in the proportion of 41.5 per cent gray, long; 41.5 per cent black, vestigial; 8.5 per cent gray, vestigial; and 8.5 per cent black, long owing to the supposed fact that crossing over between these points occurred in 17 per cent of the germ cells of the female. To clinch the matter or to establish this supposed fact we need cytological evidence that it actually occurs.

This is difficult to get because the chromosomes and their various parts generally lack distinguishing marks. However, Stern, working with Drosophila, and Creighton and McClintock, working with maize, have furnished this proof. Stern found a strain of Drosophila in which a portion of the Y chromosome had been broken off and become attached to an X chromosome. He found another strain in which a portion of an X chromosome had been broken off and become attached to the IV chromosome. A cross between these two races gave him a race in which both the X chromosomes had distinguishing marks and could be differentiated microscopically from all ordinary X chromosomes. Stern now made up a stock of flies that had the genes for carnation eye color and the bar eye pattern in the upper end of the broken X chromosome and the gene for red eyes and round eye pattern in the upper end of the X chromosome with the attached piece of the Y chromosome, the red eye and the bar pattern being dominants.

Red-eyed and bar-eyed females of the genetic constitution $crB^*/++$ were then mated to males of the genetic constitution $cr+$ *i.e.*, round eyes of carnation color in their only X chromosome (round being the wild-

* The bar-eyed mutation behaves as a dominant.

type eye shape but recessive to the mutant bar pattern). From this cross we would expect four types of females if crossing over between the two pairs of genes for eye color and eye shape had occurred. Stern secured the expected four classes of females, *viz.*, carnation, bar; red,

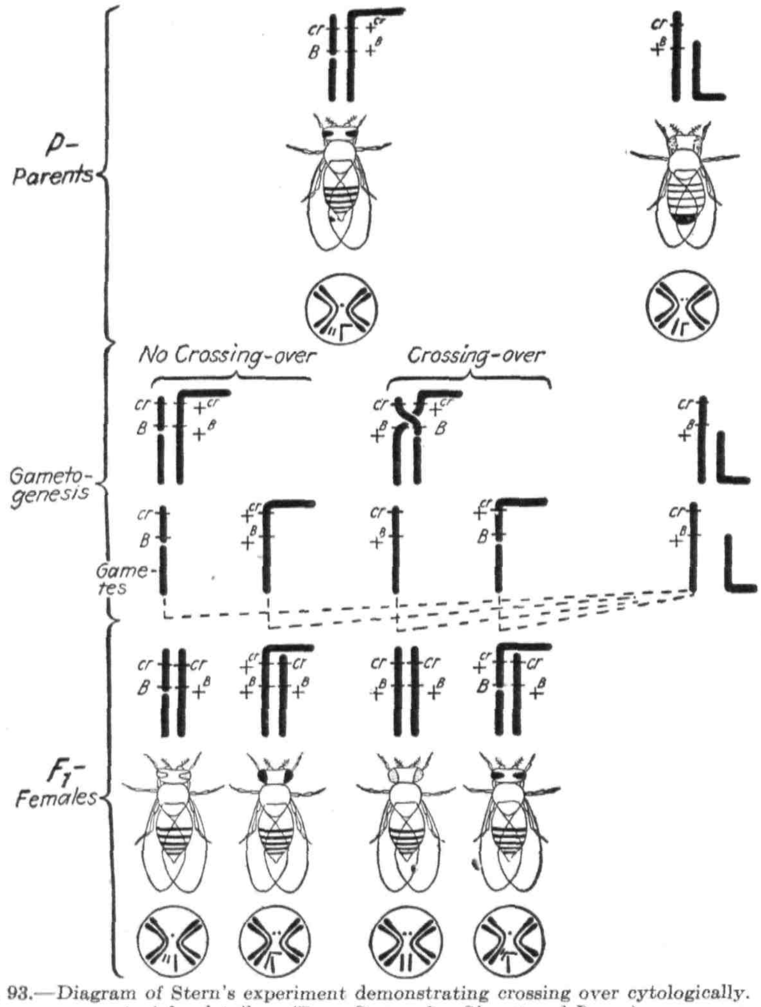


Fig. 93.—*Diagram of Stern's experiment demonstrating crossing over cytologically. See text for details. (From Stern, after Sinnott and Dunn.)*

round; carnation, round; and red, bar. The first class should have had the broken X chromosome plus a normal X from the male. The second should have had one X chromosome with the attached piece of the Y chromosome plus a normal X from the male. The third should have had two normal X chromosomes, one from the male and the other as the

result of crossing over between the two marked chromosomes of the female at a point between the two genes being considered, whereas the fourth should have had one normal X from the male plus a broken X chromosome with the piece of the Y chromosome attached to one of the pieces.

These are the results which should obtain if there had been an interchange between the two X chromosomes of the mother at a point near the upper end of the X and between the locations of the *cr* and *B* genes. Of the F_1 female flies, 364 were tested by Stern and in all but 5 (and these presumably the result of experimental error) there was a complete correspondence between the genetic and the cytological facts. In other words, genetic crossing over was proved to be accompanied by cytological crossing over, an actual exchange of material between homologous chromosomes.[1]

Linear Order of Genes.—We have seen in the two preceding sections that blocks of genes or sections of homologous chromosomes sometimes interchange their positions in the chromosomes so that new combinations

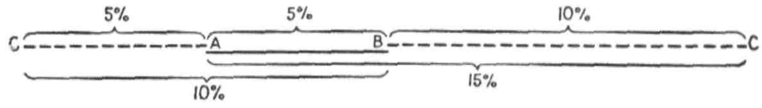


FIG. 94.—Locating gene *C* when crossover percentage between *A* and *B* is 5 per cent and that between *B* and *C* is 10 per cent.

of genes can be formed, even though the genes controlling these characters are not in separate chromosome pairs. We learned too that the percentage of the crossing over can be easily ascertained by dividing the total crossovers by the total population.

Now, if we assume that the chromatids are as likely to form chiasma, with resulting interchange, at one point as at another, then the percentage of crossing over can be taken as the measure of the distance between the genes being studied. For, if crossing over is as apt to occur at one point as at another then there will be less likelihood of a break occurring between two closely spaced genes than between two more widely spaced ones.

For example, it has been found by Morgan and his coworkers that the crossover percentage between the genes for yellow body color and white eyes is 1.5 per cent and that between white eyes and bifid wings is 5.5 per cent. Further crosses involving yellow body color and bifid wings gave a crossover value of 7.0 per cent. Now the simplest explanation of these results is that these genes lie in a straight line, for no other geometric configuration would explain the results equally well. If, therefore, we know that three genes are in the same chromosome, because they all show linkage, and breeding results show that the crossover

[1] SINNOTT, EDMUND N., and DUNN, C., "Principles of Genetics," p. 222, McGraw-Hill Book Company, Inc. New York, 1939.

percentage between genes *A* and *B* is 5 per cent and that between *B* and *C* is 10 per cent, then we can predict that the crossover percentage between *A* and *C* will be either 15 per cent or 5 per cent. It will be either the sum or the difference of the two already ascertained crossover percentages, depending on which side of *B* gene *C* happens to lie.

The above procedure in locating genes in a line on the basis of crossover percentages holds good only when we are dealing with genes lying fairly close together, for, if they are far removed from each other, there may be double or multiple crossing over that would becloud the actual situation. On the basis of crossover percentages, some of the chromosomes in Drosophila are over 100 units long, and obviously we could not have more than 50 per cent of crossing over, in fact, never get as much as 50 per cent.

Chromosome Maps.—By means of linkage and translocation studies, genes can be located in specific chromosomes; and, on the assumption that crossing over is as likely to occur at one point as at another in the chromosome, they can be located at definite points in the chromosome. The unit of distance is taken as 1 per cent of crossing over, so that, if gene *B* shows 5 per cent of crossing over with gene *A*, it is placed 5 units away from *A*. Obviously genes that are 100 units removed from each other do not show 100 per cent of crossing over. Thus genes "star" and "speck" in the second chromosome in *D. melanogaster* are 105 units apart on the maps (Fig. 95) but show a crossover value of only 48.7 per cent because of double and multiple crossing over. These long distances between genes are arrived at by summating the crossover percentages of genes lying fairly close together between the widely separated genes.

The recent work with the giant salivary-gland chromosomes of Drosophila has afforded the opportunity of making cytological maps of the bands that are or contain actual genes. The correspondence between the order of the genes in the genetic or crossover maps and the cytological maps is perfect. However, there appear to be discrepancies in the actual distances secured by the two methods.

The discrepancies are greatest at the centers of the two large autosomes and at the right or "bobbed" end of the X chromosome. In these regions one crossover unit corresponds to a relatively much greater distance on the physical chromosome than in other regions. It happens that these are the regions of spindle fiber attachment, and it is evident that in these places the frequency of crossing over per unit of chromosome length is low. Moreover it appears that no less than one-third of the whole length of the X chromosome, at the spindle-fiber end, is inert in the sense of containing practically no known gene loci (only bobbed near the end) and very little crossing over occurs in it. The crossover distance from the locus of carnation (*cr*) to the end is only about 7 units (10 per cent of the genetic length), yet this region comprises over 30 per cent of the metaphase chromosome. Near the spindle-fiber attachments of the II and III

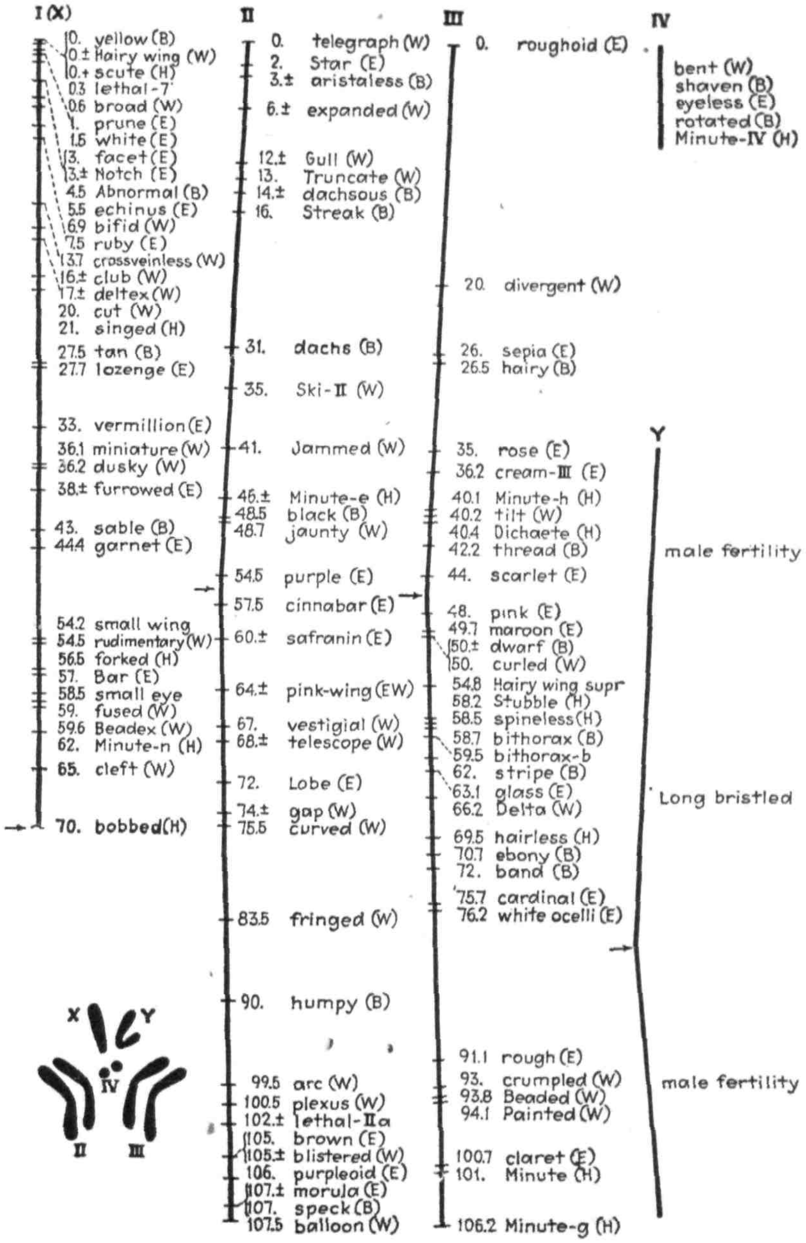


FIG. 95.—Linkage map for *Drosophila melanogaster*, showing relative positions of many of the known genes in the chromosomes as determined genetically. The letters in parentheses indicate the portion of the fly in which the characters appear: *B*, body; *E*, eye; *H*, hairs; *W*, wings. The arrows indicate positions of spindle-attachment regions. In the *Y*-chromosome, "Long bristled," which is the normal allelomorph of "bobbed," and the two factors for male sterility have not been precisely located. In chromosome IV the genes are all very closely linked. [*From Sharp, adapted from Morgan, Sturtevant, and Bridges* (1925) *and Stern* (1929).]

chromosomes there are also inert regions. It seems clear then that the unit of measure in the crossover maps is a variable one and that the amount of crossing over in any region is related to its proximity to the spindle-fiber attachment and to other regional peculiarities in the chromosomes.

By studying various inversions, translocations, deficiencies, and duplications in the salivary chromosomes of flies with known mutant genes, Painter, Bridges, Demerec, and others have been able to specify the physical location of a number of genes. A recent salivary map of the X chromosome, compared with the crossover map, is shown in Fig. 98. The gene order is the same in both maps, and the relations between crossover values and physical distance vary as they do when the metaphase map is used. The inert region of the X appears in the salivary chromosome only as a few faint bands at the spindle fiber end; and probably consists, as does the Y chromosome, chiefly of heterochromatin, that is, chromatin which does not respond to the chromatin stains used. Thus those portions that contain few or no mutant genes are also structurally different from the gene-bearing portions.

In a few cases individual gene loci have been identified with individual bands, suggesting that these are or contain the actual genes.[1]

The chromosome map of Drosophila is the most complete at present, but that of the 10 chromosome pairs in corn is growing rapidly. These maps have grown out of thousands of breeding experiments and must be acknowledged as among the most ingenious things the mind of man has ever contrived.

Interference and Coincidence.—We have seen that crossing over may take place between two nonsister chromatids at synapsis, which gives rise to recombinations of genes, although they are located in the same chromosome, and that these crossover percentages are taken as the measure of the distance between the genes in constructing chromosome maps based on the assumption that the crossing over is as apt to take place at one spot as at another. If two genes are very close together in the chromosome, they might show complete linkage, *i.e.*, the chromosome might never break between them. Likewise, if genes are very far apart, there might be two breaks, or crossovers, between them, so that in spite of this they would still be in the same chromosome and appear as if no crossing over had occurred between them. Therefore, the maps are built up on the basis of crossing over between genes that lie relatively close together, up to 10 units.

With three pairs of genes *A*, *B*, and *C* that were located in the same chromosome we might get the sorts of combinations shown in Fig. 96

Now, if we were studying the linkage relations between genes *A* and *C*, types I and IV above would appear similar genetically because genes *A* and *C* and *a* and *c* occur together. It is evident, therefore, that, if genes are relatively far apart in the chromosome, there will be more

[1] *Ibid.*, pp. 232–233.

actual cytological crossing over than is apparent genetically, because of double crossing over, and that allowance must be made for this fact mathematically.

If breeding experiments had shown genes *A* and *B* (Fig. 96) to have a linkage value of 20 per cent and genes *B* and *C* 10 per cent, then we would expect that genes *A* and *C* would show a linkage value of 30 per cent if no double crossing over took place. However, genes *A* and *C* are far enough apart so that double crossing over is possible and would infrequently occur. Such double crossing over would still leave genes *A* and *C* and *a* and *c* in the same chromosomes, the first marked by containing gene *b*, the second by containing gene *B*, so that each double crossing over hides or masks two actual crossovers. If, then, in the backcross we secured 70 per cent of type I, noncrossovers; 19 per cent of type II and 9 per cent of type III, single crossovers; between *A* and *C*; and 1 per cent of type IV, double crossovers between *A* and *C*, we would have to add

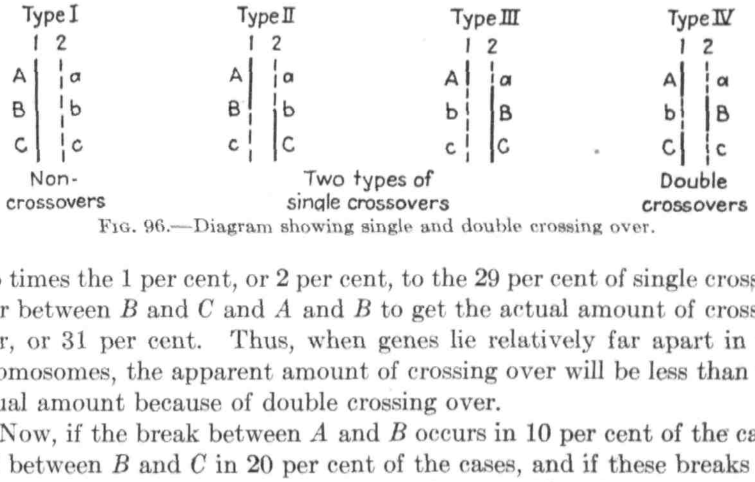


FIG. 96.—Diagram showing single and double crossing over.

two times the 1 per cent, or 2 per cent, to the 29 per cent of single crossing over between *B* and *C* and *A* and *B* to get the actual amount of crossing over, or 31 per cent. Thus, when genes lie relatively far apart in the chromosomes, the apparent amount of crossing over will be less than the actual amount because of double crossing over.

Now, if the break between *A* and *B* occurs in 10 per cent of the cases and between *B* and *C* in 20 per cent of the cases, and if these breaks are entirely independent of each other, then they should both occur 10 × 20, or in 2 per cent of the cases, for the likelihood of two independent events occurring at the same time is the product of the likelihood of each occurring separately. We saw, however, that the break occurred in both places in only 1 per cent of the cases.

Varying degrees of less than expected double crossing over are usually secured. That is to say, these breakings and crossings over in different regions of the chromosomes are not independent events but are influenced by each other so that if a break occurs between any two given genes, *e.g.*, *A* and *B*, the likelihood of a break occurring between *B* and *C* is somewhat reduced. A break at a given point in a chromosome protects the contiguous region from any breakage. This principle is known

as *interference.* If three genes lie very close together in a chromosome, we may get breaks between the first and second or between the second and third pairs but never between both the first and second and the second and third simultaneously, *i.e.*, no double crossing over. Such a situation holds, for example, between the mutant genes yellow (body), white (eyes), and bifid (wings) in the X chromosome of Drosophila, which show 1.5 per cent of crossing over between yellow and white and 5.5 per cent of crossing over between white and bifid. Here, if the events were independent, we would expect both to happen in 1.5 × 5.5 or 0.08 per cent of the cases. Interference is sometimes expressed as a coefficient of coincidence, which is secured by dividing the actual proportion of double crossovers by the expected proportion. In the above case we would have

$$\text{Actual } \frac{0}{0.0008} = 0, \text{ the coincidence value}$$

A coincidence value of 0 means that interference is complete. Likewise a coincidence value of 1 would mean no interference or complete independence of crossing over between the two regions of the chromosome. In the other example cited earlier in this section, the actual proportion of double crossing over was 1 per cent, the expected 2 per cent thus giving a coincidence value of 0.5.

Limitation of the Linkage Groups.—We have now discussed six Mendelian principles, *viz.*, segregation, independent assortment, linkage, crossing over, linear order of the genes, and interference. There is one final principle to be added to this list known as *limitation of the linkage groups.* In *Drosophila melanogaster,* four linkage groups are known; *viz.*, a large group of sex-linked genes located in the I chromosome, two large groups of autosomal genes in the large II and III chromosome pairs, and a small group of genes located in the small IV chromosome pair.

TABLE 21.—LINKAGE-GROUP RELATIONS

Species	Chromosome pairs	Known linkage groups
Drosophila melanogaster	4	4
D. willistoni	3	3
D. pseudobscuria	5	5
D. virilis	6	6
Corn	10	10
Pea	7	7
Tomato	12	10
Morning glory	15	12
Mouse	20	15
Rabbit	22	11

Each new mutant in Drosophila has proved to be linked to other genes in one or another of these four pairs of chromosomes. Such findings are of course basic to the validity of the fundamental theory of chromosomal inheritance. Obviously, if a fifth group of genes were ever discovered in *D. melanogaster*, the whole theory of chromosomes and genes would have to be entirely revamped or discarded.

Table 21 shows the linkage-group relations in several species.

Application to Farm Animals.[1]—The foregoing principles of inheritance have been worked out from breeding experiments with plants, insects, or small laboratory animals. These species reproduce rapidly, have large numbers of offspring, and are inexpensive to grow. None of these three features holds with our larger farm animals.

The principles have been and are being used, however, to explain various types of inheritance in the larger farm mammals. Up to the present, no contradictions to established principles have been found, although in many instances the principles must be applied in general rather than in specific ways. Unfortunately in the higher animals we have large numbers of chromosome pairs and small numbers of offspring. This, together with the fact that the environment is so diverse and its influence in many cases so great, leads to many difficulties in applying the known principles in any detailed manner.

A knowledge of basic principles and an assurance that they hold for all living forms gives the animal breeder a firm foundation on which to base his breeding operations. At least the main routes toward his goal of beautiful form and efficient function are now more clearly delineated and should prevent his choosing an entirely wrong road or taking too many expensive and time-wasting detours.

Genes and Development.—It will be recalled that in Chap. XII we listed three problems of genetics. One of these had to do with the actual nature of the genes, about which very little is known at the present. Another had to do with the modes of inheritance between ancestors and offspring, with which the past three chapters have dealt and with which the three following chapters will be concerned. The third problem listed was that of the manner in which the characters latent in the zygote became patent in the resulting offspring.

Thus far we have talked about genes and about their final end products, characters, without attempting to say how the genes finally come to express themselves as they do, or, in other words, what the causal relation is between genes and chromosomes and expressed characters. We have pointed out that development results from the actions and interactions of genes, cytoplasm, and environment, and that, although certain genes are known by some final character, there are often

[1] See Appendix A for references on inheritance in farm animals.

as *interference*. If three genes lie very close together in a chromosome, we may get breaks between the first and second or between the second and third pairs but never between both the first and second and the second and third simultaneously, *i.e.*, no double crossing over. Such a situation holds, for example, between the mutant genes yellow (body), white (eyes), and bifid (wings) in the X chromosome of Drosophila, which show 1.5 per cent of crossing over between yellow and white and 5.5 per cent of crossing over between white and bifid. Here, if the events were independent, we would expect both to happen in 1.5 × 5.5 or 0.08 per cent of the cases. Interference is sometimes expressed as a coefficient of coincidence, which is secured by dividing the actual proportion of double crossovers by the expected proportion. In the above case we would have

$$\text{Actual}\ \frac{0}{0.0008} = 0, \text{ the coincidence value}$$

A coincidence value of 0 means that interference is complete. Likewise a coincidence value of 1 would mean no interference or complete independence of crossing over between the two regions of the chromosome. In the other example cited earlier in this section, the actual proportion of double crossing over was 1 per cent, the expected 2 per cent thus giving a coincidence value of 0.5.

Limitation of the Linkage Groups.—We have now discussed six Mendelian principles, *viz.*, segregation, independent assortment, linkage, crossing over, linear order of the genes, and interference. There is one final principle to be added to this list known as *limitation of the linkage groups*. In *Drosophila melanogaster*, four linkage groups are known; *viz.*, a large group of sex-linked genes located in the I chromosome, two large groups of autosomal genes in the large II and III chromosome pairs, and a small group of genes located in the small IV chromosome pair.

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iodine, whereas pollen from mutant waxy plants stains reddish brown owing to the production of a different enzyme. When a cross is made between starchy and waxy, however, the hybrid produces two sorts of pollen, the one with the starchy gene staining blue, the other with the waxy gene reddish brown.

In some cases the genes delay their action for a short while. In the higher species the anlagen of both male and female genitalia are present after the first few weeks of embryonic life. Then apparently the different

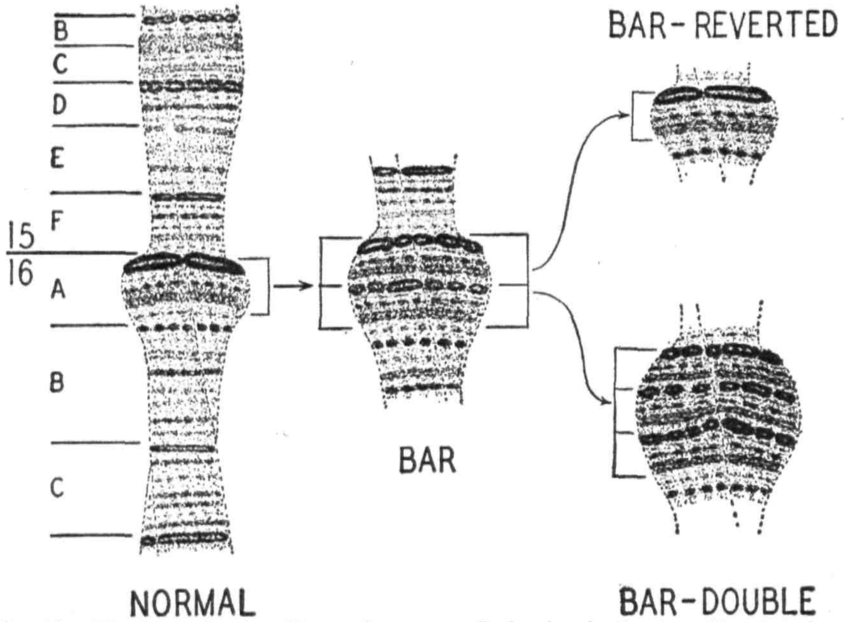

FIG. 97.—The bar region in salivary chromosome I, showing duplication of bands in bar and double-bar. (*From Bridges, after Sinnott and Dunn.*)

gene complexes come into play, and the primordia of one sex develop to maturity, whereas those of the other atrophy. There are other characteristics that may remain latent for a considerable time after birth, and some do not appear until middle life or later.

Sturtevant and Morgan first reported a case in which the position of a gene in a chromosome apparently affects the expression of a character. This is known as *position effect*, and an example is the bar gene in Drosophila. Bar eye in Drosophila (facets in a bar pattern rather than round) has long been known as a dominant at point 57 in the X chromosome. Zelany discovered that homozygous bars very infrequently produced a normal (1 in 1,500), and, still less frequently, a still more restricted bar, or ultra or double bar. By using bar females with two other mutant genes near bar, Sturtevant and Morgan showed that the production of

normals from bar was always due to a peculiar unequal crossing over. Bridges finally, through a study of salivary-gland chromosomes, showed normal round eyes to be due to one band in the X chromosome, bar to a duplication of this band, and double bar to this band being in triplicate.

In leaving this entrancing but difficult field of the basis of genic, cytoplasmic, environmental, enzymatic, hormonal, and organizational influences in the development and organization of new characters into a completed unique whole (epigenesis), we would remind the student that any individual begins its life as a tiny fertilized egg, but that very soon the complete body pattern emerges in a very minute form, but it is definitely organized. The month-old embryo is only a few centimeters long but is definitely organized as a miniature of the adult form. All of its parts and organs are at this time closely related in space, were even more so earlier, so that the influence of one portion or organ of the body on contiguous ones is not difficult to imagine. Spemann's classic experiment in transplanting a tiny portion from near the dorsal lip of the blastopore of an early embryonic amphibian to a totally different location in another embryo with the resulting formation of a new embryo out of tissues that would normally have produced totally different structures was the first indication of definite organizing centers in the developing embryo.

It must be admitted that but little is yet definitely known of the causes bringing about differentiation and specific organization in a developing embryo, but much research is now in progress to bridge the void between the genes in the zygote and the fully developed character in the resulting organism.

Evidence Supporting Gene Theory of Inheritance.—There are many lines of evidence lending support to the chromosomal, or gene, theory of inheritance. First and foremost is the fact that almost all organisms arise from the union of an egg from the female parent and a spermatozoon from the male parent. This is all the living material the offspring gets from its parents, though, of course, it derives its materials for growth (proteins, fats, minerals, etc.) from its mother's blood. Results of breeding experiments show that, speaking generally, both parents are jointly and equally responsible for the potentialities of their offspring. Because this is so and because the two germ cells, egg and sperm, are alike only as to their nuclei, it seems logical to conclude that the determiners of potentialities are located in the two nuclei which contain the chromosomes and which in turn are made up of genes.

Additional support for the theory is to be found in the phenomenon known as *parthenogenesis; e.g.*, an organism arising from an egg that has been stimulated to cell division artificially; *e.g.*, with a hot needle. These organisms evidence maternal characteristics only. In like manner an

egg, the nucleus of which has been removed or inactivated by X rays, may be fertilized by a sperm, and in this case the organism will evidence paternal characteristics only.

Further evidence is available from cytological studies, which have demonstrated that, if one of the small (IV) chromosomes in Drosophila is lost from an egg or sperm, the resulting offspring is different from a normal fly in many parts of the body; *i.e.*, specific effects are produced by this IV chromosome. For example, if a female with normal eyes but having only one IV chromosome is mated with a mutant eyeless male, half the offspring are eyeless, and they are also weak individuals, many of them not getting through the pupal stage successfully. This proves that the gene for the eyeless condition is located in the small IV chromosome.

The behavior in inheritance of sex-linked characters, *i.e.*, characters determined by genes located in the sex chromosomes, is additional strong evidence that the genes located in the chromosomes of the nuclei of the sex cells, ova and spermatozoa, are the actual determiners of the potentialities of any organism.

Finally the work of Stern, with Drosophila, and Creighton and McClintock, with maize, which demonstrates a complete correspondence between genetic and cytological crossing over, seems to furnish the final bit of positive proof for the complete substantiation of the chromosomal, or gene, theory of inheritance.

Summary of Modern Genetic Theory.—The modern theory of inheritance is based upon the behavior in gametogenesis and ontogeny of more or less hypothetical entities called *genes*. However, the theory has now been tested by means of thousands of planned breeding experiments and has been corroborated by numerical data, as indicated in the definite numerical ratios for the mono-, di-, tri-, and polyhybrids. In other words, the theory is no longer a theory but an established fact. It should be recalled that the facts of breeding came first and the theory to explain the facts came second. We demand two things of any theory: (1) that it logically explain events that have transpired in the past, and (2) that its principles enable us successfully to predict future happenings. These criteria of fitness have been successfully met by the chromosomal, or gene, theory of inheritance.

In brief, the gene theory assumes that the characteristics of an organism are conditioned by paired genes located at similar loci in homologous chromosomes; that one member of a gene pair may dominate the situation more or less fully in the developed organism, so that the other member of the pair is not externally recognizable; that the genes are organized into groups, each group forming a chromosome; that at the reduction division in gametogenesis one member of each homologous pair of chromosomes is found in each daughter cell; that the distribution

of the homologous chromosomes to the daughter cells is at random; that previous to reduction, *i.e.*, during synapsis, equal interchanges of chromatin material may take place between the nonsister chromatids; and that the chromosomes are always organized in a definite manner, each gene in its inviolable place and the genes arranged in a linear series.

Later chapters will indicate how the genes may change, thus giving rise to new variates. Once again the writer would like to caution against any tendency to oversimplify the matter of the genes and their behavior in inheritance. The genes themselves are probably very complex in their structure. They are very closely associated with the cytoplasm of the cells, and full development of the individual should be looked upon as a result of the interactions between the genes themselves, between the genes and the cytoplasm of the cells, and between the cells and their environment. It is the interactions and interrelations of all these forces that function in the development of a new individual rather than the individual actions of separate genes.

It is known, for instance, that in Drosophila at least 50 pairs of genes function in bringing about the development of the normal red eye. It is also known that a change at locus 44.4 in the I chromosome, a change at locus 54.5 in the II chromosome, or a change at locus 49.7 in the III chromosome will each result in purplish rather than red eyes. These genes have been named *garnet, purple,* and *maroon,* respectively. It would be possible, therefore, to mate two purple-eyed individuals and to get from them all normal red-eyed offspring, for each parent might supply the missing normal gene that the other lacks. It is also readily seen that one type of purplish eyes (garnet) would show sex-linked inheritance, for this gene is located in the sex chromosome, whereas the other two sorts of purplish eyes (purple and maroon) would show ordinary Mendelian inheritance.

As has been shown earlier, dominance is a relative term, and a characteristic that is dominant in one type of mating may be recessive in another. Inheritance, therefore, should be looked upon as the interaction between genes, cytoplasm, and environment rather than thought of in an absolute sense.

Summary.—In this final chapter dealing with the principles of inheritance, we have considered the complications introduced into breeding data by the fact that many genes may be located in one chromosome, so that these genes do not assort independently, although the chromosomes always do so. We have seen that varying degrees of linkage up to 100 per cent may be encountered. If linkage is not complete, various amounts of crossing over up to nearly 50 per cent may be encountered, and crossover values between any two genes remain constant under uniform conditions. The use of crossover values in constructing the very

ingenious chromosome maps was indicated on the basis of the genes being arranged in linear series along the chromosomes. We completed our discussion of the seven Mendelian principles with references to interference and to limitation of the linkage groups to the number of pairs of chromosomes present in any species. Finally, we discussed the as yet rather incompletely known role of the genes in development, indicated the various lines of evidence that substantiate the chromosomal and gene theory of inheritance, and presented a summary of the modern genetic theory.

References[1]

Problems

1. Assume that genes *a* and *b* are linked and show 40 per cent of crossing over. If a ++/++ individual is crossed with one that is *ab/ab*, what will be the genotype of the F_1? What gametes will the F_1 produce and in what proportions? If the F_1 is crossed with a double recessive, *ab/ab*, what will be the appearance and genotypes of the offspring?

2. If the original cross is $+b/+b \times a+/a+$, what will be the genotype of the F_1? What gametes will it produce? If the F_1 is crossed back with a double recessive, what will be the appearance of the offspring?

3. An individual homozygous for genes *cd* is crossed with wild type and the F_1 crossed back to the double recessive. The appearance of the offspring is as follows: 903 ++, 898 *cd*, 98 +*d*, 102 *c*+. Explain this result, giving the strength of the linkage between *c* and *d*. If assortment between *c* and *d* were independent, what would be the result of this cross?

4. If the cross in the preceding question had been between a homozygous +*d* individual and a homozygous *c*+ one, what would be the result of the cross between F_1 and the double recessive?

5. How far apart are *A* and *B* if in the F_2 you derive 706 *AB*; 291 *Ab*; 304 *aB*; 697 *ab*?

6. Results of a cross of *Aa Bb Cc* × *aa bb cc* give:

600 *ABC*	1[illegible] *aBC*	15 *aBc*
580 *abc*	120 *Abc*	5 *Abc*
	130 *abC*	
	120 *ABc*	

What are the percentages of crossing over between *A* and *B* and *B* and *C*? How far apart are A and *C*?

7. Note.—In Drosophila the mutant known as *black*, *b*, has a black body in contrast to the wild type, which has a gray body; and the mutant *arc*, *a*, has wings which are somewhat curved and bent downward, in contrast to the straight wings of the wild type.

In the two following crosses the parents are given (homozygous in each case) together with the counts of the offspring of F_1 females bred to black, arc males (data from Bridges and Morgan).

[1] See lists at end of Chaps. XII and XIII.

a. Black, arc × wild type (gray, straight)

F_1 females × black, arc males give

1,641 gray, straight.
1,251 gray, arc.
1,180 black, straight.
1,532 black, arc.

b. Black, straight × gray, arc

F_1 females × black, arc males give

281 gray, straight.
335 gray, arc.
335 black, straight.
239 black, arc.

From these data calculate the crossover value between black and arc.

8. Note.—In Drosophila the mutant known as *vestigial*, *v*, has wings that are very much reduced as compared with the long wings of the wild type.

In the two following crosses the parents are given, as in the previous question, together with the counts of offspring of F_1 females crossed with black, vestigial males (data from Bridges and Morgan).

a. Black, vestigial × wild type (gray, long)

F_1 females × black, vestigial males give

822 gray, long.
130 gray, vestigial
161 black, long.
652 black, vestigial.

b. Black, long × gray, vestigial

F_1 females × black vestigial males give

283 gray, long.
1,294 gray, vestigial.
1,418 black, long.
241 black, vestigial.

From these data calculate the linkage strength between black and vestigial.

9. Note.—In tomatoes, Jones has found that tall vine is dominant over dwarf, and spherical fruit shape over pear. Vine height and fruit shape are linked, with a crossover percentage of 20 per cent.

If a homozygous tall, pear-fruited tomato is crossed with a homozygous dwarf, spherical-fruited one, what will be the appearance of the F_1? Of the F_1 crossed with a dwarf, pear? Of the F_2?

10. A certain tall, spherical-fruited tomato plant crossed with a dwarf, pear-fruited one produces 81 tall, spherical; 79 dwarf, pear; 22 tall, pear; and 17 dwarf, spherical. Another tall, spherical plant crossed with a dwarf, pear produces 21 tall, pear; 18 dwarf, spherical; 5 tall, spherical; and 4 dwarf, pear. What are the genotypes of these two tall, spherical plants? If they were crossed, what would their offspring be?

11. NOTE.—In rats dark eyes are due to the interaction of two genes *R* and *P*, the recessive allele of either producing light eyes. These genes are in the same chromosome.

When homozygous dark-eyed rats, $++/++$, were crossed with double-recessive ones, rp/rp, and the F_1 crossed back with the double recessive, the following offspring were obtained (data from Castle): 1,255 dark-eyed; 1,777 light-eyed.

When $+p/+p$ animals were crossed with $r+/r+$ ones and the F_1 crossed back with the double recessive, the following offspring were obtained: 174 dark-eyed; 1,540 light-eyed.

Calculate the linkage between *r* and *p*.

12. In the fowl, assume that *e* (early feathering) and *B* (barring) are sex-linked and show 20 per cent of crossing over (in the male only). If a male from a cross of late-feathered, barred male with early, black female is mated with an early, black female, what will be the appearance of their offspring, as to feathering and barring?

13. Assume that genes *a* and *b* are linked, with a crossover percentage of 20 per cent; and that *c* and *d* are also linked, with a crossover percentage of 10 per cent, but are in another chromosome. Cross a plant homozygous for *ABCD* with one which is *abcd* and cross the F_1 back on *abcd*. What will be the appearance of the offspring of this cross?

14. In Drosophila, yellow body is sex-linked and recessive to the gray body of the wild fly. Vermilion eye is also sex-linked and recessive to the wild red eye. The genes for yellow and vermilion show about 28 per cent of crossing over. The gene for vestigial is in one of the autosomes. If a homozygous yellow-bodied red-eyed long-winged female is crossed with a homozygous gray-bodied vermilion-eyed vestigial-winged male, and if an F_1 female is crossed with a yellow, vermilion, vestigial male, what will be the appearance of the offspring of this last cross?

CHAPTER XVI

THE PRINCIPLES OF VARIATION

Genetics, as was said earlier, is concerned with heredity and variation. Its task is to explain why an organism does or does not resemble its ancestors. The three previous chapters have dealt with hereditary likenesses between related organisms. Heredity is the great conserving force. The fact that the genes and their combinations are relatively stable has acted as a ratchet mechanism to hold whatever gains have been made from the standpoint of evolution. For progress, however, we need something more than this, *viz.*, variation. For many centuries, species and varieties were believed to be immutable. The rise of many varieties of dogs from one or two remote ancestors by means of the principles of variation and selection and the same phenomenon in horses, cattle, sheep, and swine was pointed out in an earlier chapter.

Henry van Dyke is reported to have said that there is one thing in which all men are exactly alike, and that is that they are all different. This statement also holds true for farm animals. To the observing it is quite evident that "the most invariable thing in nature is variation."

When we consider that probably no two blades of grass, no two calves, and no two human beings have ever been just exactly alike (though identical twins are essentially so), we get a fleeting glimpse of the resourcefulness of nature. It would seem that the new plans and specifications must sometime be depleted, yet life flows along in its thousands of varieties and millions of unique individuals, each different from all the rest of its kind. Fortunate, too, that this is so, because without this principle progress would be impossible. As has been said, "Variation is at once the hope and the despair of the breeder," the hope because through it may be produced offspring better than their parents, the despair because after animals have been greatly improved, they may and very often do vary again toward mediocrity.

That animals vary in size, type, rate of growth, efficiency of feed conversion, quality of carcass, proportion and distribution of fat and lean, wool quality and quantity, fertility, longevity, resistance to disease, milk production, butterfat percentage, color of milk, persistency, speed, stamina, style, tractability, color, and in a hundred other ways is too evident to need much discussion.

Here are two steers, one of them gains 22.1 lb. for each 100 lb. of nutrients fed; the other only gains 14.3 lb. from a like amount of feed.

Here are the litters of two sows, one of them gains 100 lb. from 504 lb. of feed; the other litter gains 100 lb. from 360 lb. of feed.

Here are two dairy cows, one of them returns 36 lb. of total digestible nutrients for each 100 lb. fed; the other returns only 18 lb. from a like amount of feed.

Here is a Guernsey bull bred to 8 cows that range from 12,500 to 13,500 lb. of milk per year; the 8 daughters range from 8,600 to 15,600 lb.

Here is an Ayrshire bull bred to 13 cows that range from 10,500 to 11,500 lb. of milk per year; the 13 daughters range from 7,800 to 15,300 lb.

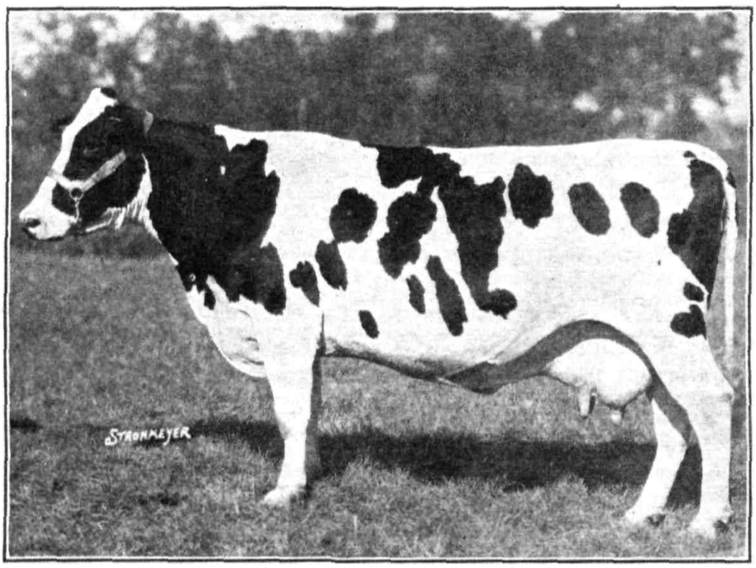

FIG. 99.—Beth of Amherst 3rd., a Grand Champion at Eastern States Exposition (picture taken when dry). Her twin sister was nearly as poor a dairy type as this one is good.

Variation is tremendous, partly owing to the mechanism of inheritance, partly to the effects of environment. Most of the qualities of our animals are elastic. Depending on feed, care, etc., a cow may produce 8,000 lb. of milk in a year or 16,000 lb. A sow may farrow ten 3-lb. pigs and raise them all, or seven 2-lb. pigs and raise four of them. The breeder's task is to provide the best possible environment at all times and to make the environment as uniform as possible in order that his variations will be known to have a genetic basis.

Causes and Types of Variation.—There can conceivably be but two causes of genetic variation. It is caused either by some outside, supernatural force, or else it is inherent in the nature of living things, their natural response to stimuli.

Variations { Supernatural
Variations { Natural

General opinion leans toward the latter explanation. There are two types of stimuli that might conceivably bring about variation, one internal, the other external to the organism. Any fully developed organism is the result of the combined action of these internal and external stimuli.

Variations { Autogenetic
Variations { Exogenetic

The organism starts as a single-celled zygote, with its full complement of genes derived from both paternal and maternal sources. This genetic heritage has a tendency to develop in a certain definite way, owing to its chemical and physical make-up. The norm for this new individual may vary from that of one or both of its parents because of its different chromosomal content. During intrauterine development, any organism is subject to various influences from its mother, with whom it lives in very close association. Chemical products in the blood of the mother may be transfused into the circulation of the embryo and may react in various ways on the developing embryo or cause it to react in a variety of ways. The mother's blood, or the fluid surrounding each cell, may contain nutritive material that will assist in the proper growth and full development of the embryo. On the other hand, they may contain waste or toxic products, secretions or hormones from various glands, etc., any of which may cause the embryo to vary more or less from its original normal tendencies. Effects due to the parent's habits or to contingencies in the developing embryo itself cause many variations to appear in the fully developing organism, all the way from a doubling of parts, through various types of changes, including blemishes and malformations to an entire pinching off or absence of the part.

Variations { Germinal { Recombinations
Variations { Germinal { Gene and chromosome mutations
Variations { Somatic { Changes in soma, behavior, etc.

In this chapter, we shall consider only those variations that have their origin in the germinal material, the genes and chromosomes in the germ cells, leaving the somatic variations to be treated in the next chapter.

Variation as a Tool.—Variation is one of the most useful tools that the breeder possesses. It provides him the raw material from which he can fashion better animals. The breeder is constantly on the lookout for desirable types of variation. He sees variation as it manifests itself in his animals and seizes upon it in the hope that it will prove to be hereditary. Much variation does have a genetic basis, much of it too is environmental, whereas some perhaps is both. It is no simple

matter to separate these three categories. In addition to these complications is the further one that the hereditary variations may be of various sorts. Some of the allelic pairs of genes may show varying degrees of dominance, from complete to an entire lack. This same feature of dominance between different pairs of genes known as *epistasis* may be operating, whereas in still other cases the various genes may behave in a cumulative or additive fashion. To secure desirable variation of a hereditary sort and to guide it toward some preconceived ideal of perfection is the problem that the breeder constantly struggles with.

Fortunately there is generally plenty of variability available. In horses, cattle, sheep, and swine there are literally all sorts. The animals

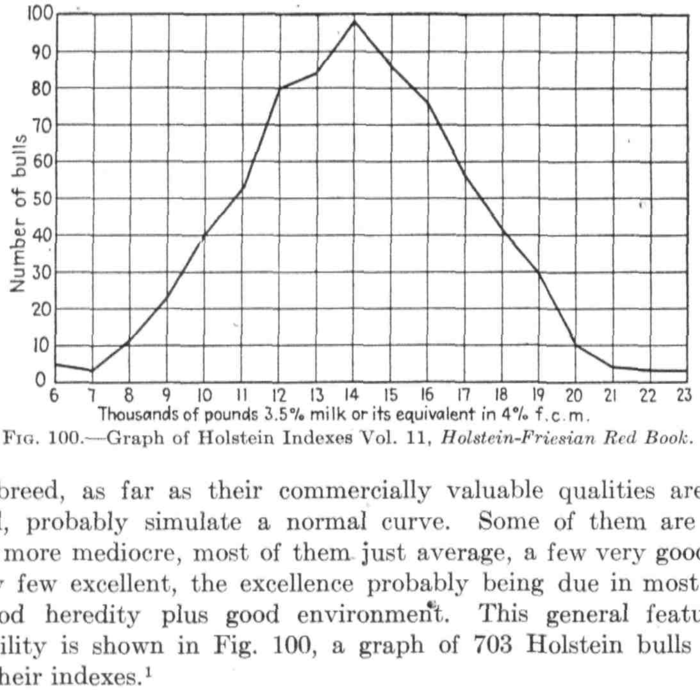

FIG. 100.—Graph of Holstein Indexes Vol. 11, *Holstein-Friesian Red Book*.

of a breed, as far as their commercially valuable qualities are concerned, probably simulate a normal curve. Some of them are poor, a few more mediocre, most of them just average, a few very good, and a very few excellent, the excellence probably being due in most cases to good heredity plus good environment. This general feature of variability is shown in Fig. 100, a graph of 703 Holstein bulls listed with their indexes.[1]

The above graph shows that 5 of these bulls had indexes of 6,000 lb. of 3.5 per cent milk, 7 had indexes of 7,000 lb. of 3.5 per cent milk, 11 indexes of 8,000 lb., etc. up to 4 bulls with indexes of 22,000 lb. and 4 with indexes of 23,000 lb. of 3.5 per cent milk. Because the index is computed from a comparison of dams' and daughters' records, it is obvious that the females would also show this sort of normal curve of production. The breeder is, of course, trying to make his selections from animals in the upper half or top quarter of these curves, and he

[1] From Vol. 11 of the "Holstein-Friesian Red Book."

hopes that a goodly part of this variation is hereditary and will be passed along to the offspring.

Freeman[1] found the mean number of body vertebrae of 52 Duroc pigs to be 20.52 ± 0.067, and for 79 Yorkshire pigs to be 21.27 ± 0.046.

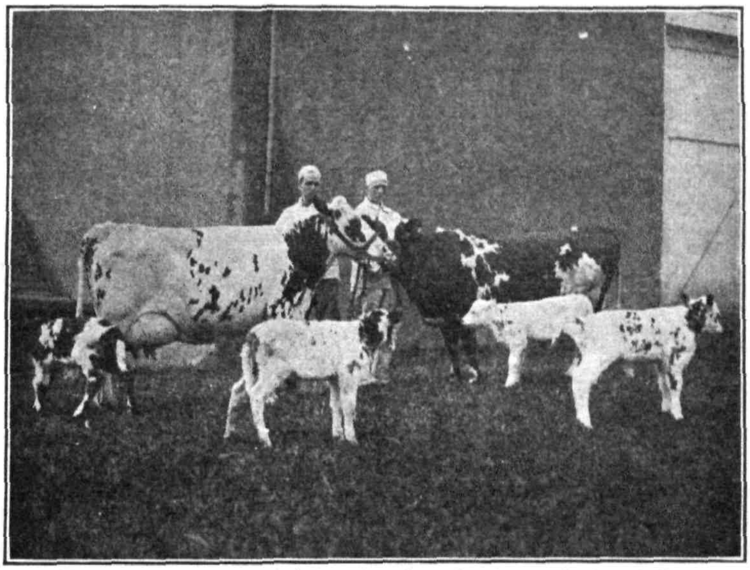

FIG. 101.—Two Ayrshire cows and their twin calves showing marked variation in amount of red color in the coat.

The increased number of vertebrae were associated with greater body length, which would add to carcass value and might possibly be correlated with greater fertility.

Variations from Recombinations.—We have already discussed pretty thoroughly the general proposition of recombinations of chromosomes during meiosis. In an organism with two pairs of chromosomes, there are four possible ways of recombining these intact chromosomes as indicated in Fig. 102.

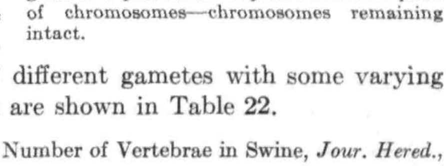

FIG. 102.—Showing the different types of germ cells possible in a species with two pairs of chromosomes—chromosomes remaining intact.

In each resulting germ cell there must necessarily be one member of each pair of chromosomes. The possible numbers of different gametes with some varying numbers of pairs of chromosomes are shown in Table 22.

[1] FREEMAN, V. A., Variations in the Number of Vertebrae in Swine, *Jour. Hered.*, **30** (2): 61–64, February, 1939.

TABLE 22.—NUMBER OF DIFFERENT KINDS OF GERM CELLS POSSIBLE FROM VARYING NUMBERS OF PAIRS OF CHROMOSOMES

	Number of pairs of chromosomes	Number of different kinds of germ cells	
Ascaris	1	2^{1}	2
A. megalocephala	2	2^{2}	4
Drosophila melanogaster	4	2^{4}	16
Corn	10	2^{10}	1,024
Swine	19	2^{19}	524,288
Human	24	2^{24}	16,777,216
Cattle, goat, horse	30	2^{30}	1,073,741,824

It is evident from the above table that the simple recombination of intact chromosomes in the higher species can account for a tremendous amount of variation. From a perusal of the above table one might conclude that breeding is a pretty haphazard and impossible task anyway. The writer would not try to maintain that it is easy, but neither is the job as impossible as might appear at first glance. What we are trying to do from a practical breeding standpoint is to make our animals pure for genes that lead to the development of desirable characters. At present they are rather heterozygous and therefore do not breed true. Two homologous chromosomes may bear the following sorts of genes.

A ( ) *a*
B ( ) *B*
c ( ) *C*
D ( ) *d*
e ( ) *e*

If, by selecting, we bring it about that these two chromosomes become homozygous,

A ( ) *A*
B ( ) *B*
C ( ) *C*
D ( ) *D*
E ( ) *E*

then it will make no difference which one of these two homologous chromosomes go to any egg or sperm, for they are now exactly similar. It would still and always be true that the 30 pairs of chromosomes in cattle could and would be capable of producing over a billion different recombinations, but, if our animals were entirely homozygous, all of these billion combinations would be identical. It seems unlikely that we can ever reach this goal, but the fact remains that the more heterozygosity can be reduced, the less variation we will have.

If a male *Aa* is mated to a female *Aa*, there can be produced two different types of gametes (*A* or *a*) by each parent and offspring of three different genotypes (*AA*, *Aa*, or *aa*).

If a male of the genetic constitution *Aa Bb* (with genes *A* and *B* in different chromosomes) is mated to a female of the same genetic make-up, there can be produced four different types of gametes by each parent and offspring of nine different genotypes.

With three pairs of heterozygous nonlinked genes in each parent, we would have eight different types of gametes and offspring of 27 different genotypes.

TABLE 23.—INDEPENDENTLY SEGREGATING GENE RECOMBINATIONS

Number of pairs of heterozygous genes	Number of different gametes	Number of different genotypes
1	2	3
2	4	9
3	8	27
n	2^n or $(10^{0.301n})$	3^n or $(10^{0.477n})$

If two animals were of the genetic constitution shown below (genes in different chromosomes),

sire, *Aa bb CC Dd*
dam, *Aa Bb cc DD*

then there would be the following possible genotypes of offspring

$$3 \times 2 \times 1 \times 2 = 12.$$

Thus we could have 12 different sorts of full brothers or sisters, as to genotype, from mating the above two parents. All of these animals would have identical pedigrees but their genotypes might all be different ranging from

AA Bb Cc DD to *aa bb Cc Dd*

If the capital letters represented desirable traits and the small letters undesirable ones, we can see that there would be a vast difference between these full sisters or brothers. Identity of pedigree, then, does not mean identity of inheritance except when the parents are homozygous for each pair of genes.

Our example has dealt with four pairs of genes, or eight in all. We do not know how many genes are present in the chromosomes of our farm animals. There are 60 chromosomes in some of these animals, and, if there were an average of 100 genes in each chromosome, there would be a total of 6,000 genes. Each parent would then be transmitting not 4

mated with a normal red-eyed female fly, the F_1 offspring were all red-eyed. In the F_2, however, the white-eyed condition again appeared, but only in male flies. This is, therefore, a sex-linked, recessive mutation. Other changes in this same gene have resulted in a series of 14 allelic

TABLE 24.—STADLER'S DATA ON THE FREQUENCY OF CHANGES IN SEVEN GENES OF MAIZE[1]

Gene	Gametes tested	Number of mutations	Average per one million gametes
R	554,786	273	492
I	265,391	28	106
Pr	647,102	7	11
Su	1,678,736	4	2.4
Y	1,745,280	4	2.2
Sh	2,469,285	3	1.2
Wx	1,503,744	0	0

[1] STADLER, *Jour. Hered.*, **24**, (10): 372, 1933.

characteristics as to eye color in Drosophila, ranging from white through ecru, tinged, buff, ivory, eosin, apricot, cherry, blood, coral, and wine to red. Reverse mutations also occur; *i.e.*, red eyes may mutate to white, and white may mutate back to red.

Some gene mutations, such as lobe 2 in Drosophila, are dominants in inheritance. A great many of the mutations are lethal, the offspring never reaching maturity, whereas in others, *e.g.*, the white-eyed mutant, many other characteristics besides eye color are affected, the white-eyed individuals being less robust, more sluggish, and shorter lived.

The best known mutation among farm animals is, no doubt, the characteristic of polledness, or hornlessness. This mutation probably arose because of a chemical change of some sort in the chromosomes. No doubt, they have arisen in all the breeds at times, and in most breeds they have been noticed and valued and a polled strain developed from them. The reason for the change in the chromosomes that prevents the horns from developing is unknown.

Another mutation, now extinct, occurred many years ago in sheep. Seth Wright, a Massachusetts farmer, had dropped in his flock a ram lamb that was a mutant, being low-backed, long-bodied, and having short crooked legs, something after the fashion of a dachshund. Farmer Wright recognized its value—its type of build, although not interfering seriously with wool production, being a decided deterrent to the sheepish pastime of fence jumping. The ram, a mutant, was used for breeding, and from this start the Ancon breed of sheep, with the characteristics

listed above, was produced, though the breed has long since been supplanted by the Merino.

The Mauchamp sheep of France, with a superior sort of fleece, are sometimes considered a mutant race, but, inasmuch as the original ram was a hybrid between a Mauchamp ewe and a Dishley ram, this case, as Nathusius points out, must be removed from the records of actual mutations in domestic animals. Another character in sheep reported from Norway, *viz.*, short ears, though of no practical importance, is perhaps, a mutant.

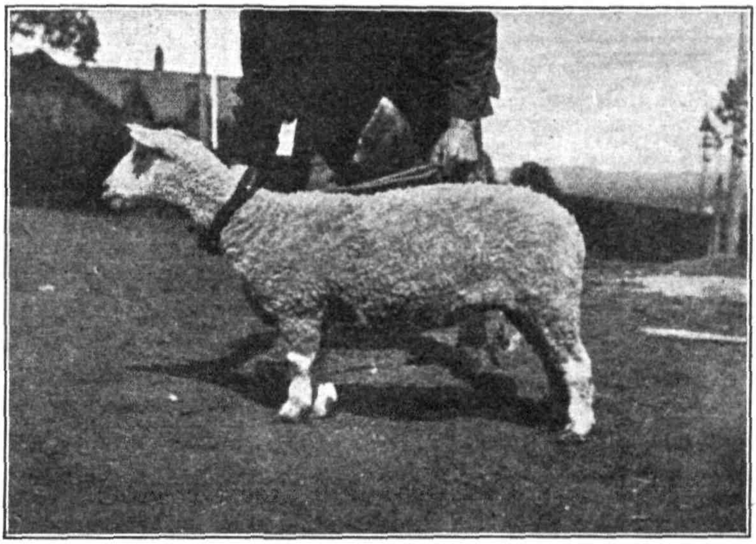

FIG. 103.—A sheep with very short and crooked legs after the style of the Ancon.

Regarding mutations in domestic animals Babcock and Clausen state that:

> Any system of herd improvement founded on the search for and utilization of mutants is doomed from the beginning to failure, for mutants of a beneficial character appear so rarely as to have almost no practical significance. If by some fortunate chance a breeder should find himself in possession of a favorable mutant individual, however, it is a simple problem in Mendelism to establish its characters in a constant race.

For instance, if a mutant sheep were produced with no tail, a tailless breed could soon be developed and the trouble of docking saved.[1] No system of breeding has yet been advocated to produce mutations, perhaps none will ever be devised. Tendency to mutate, however, is very likely

[1] See *S. Dakota Agr. Expt. Sta. Cir.* 28, 1940.

sion) they produce only *Bd* + or +*l* gametes and only *Bd*+/+*l* offspring (with an occasional ++ normal if crossing over occurs), because the *Bd*+/*Bd*+ offspring and the +*l*/+*l* offspring both die, which gives an apparently true-breeding strain because of a system of balanced lethals.

Variation from Chromosomal Aberrations.—In addition to gene or point mutations a considerable variety of chromosomal aberrations involving various-sized blocks of genes, whole chromosomes, or whole sets of chromosomes have been discovered in recent years. Changes of this nature are generally brought to light by discrepancies in breeding behavior resulting in disturbances of the normally expected Mendelian ratios, in the creation of new linkage relations, or in the appearance of variable offspring. When such things occur, cytological study has generally revealed certain changes in the number or arrangement of the loci within the whole chromosome complex or a change in the actual number of chromosomes. This close correspondence between the visible changes in the chromatin and changes in ratios or in individuals is, of course the strongest possible evidence supporting the chromosomal theory of inheritance. Since visible changes in the chromosomes result in recognizable variations in the fully developed organisms, it seems more than justifiable to assume that the chromosomes and genes are the actual determiners of potentialities.

CHANGES IN BLOCKS OF GENES

Translocation.—It sometimes happens that a chromosome becomes broken and one of the pieces attached to some other chromosome. Bridges discovered that a group of genes that normally belonged in the II chromosome suddenly showed linkage relations with genes in the III chromosome, and this was termed *translocation*. If the piece becomes attached to a nonhomologous chromosome, a new linkage relation is set up. If, for instance, a small piece of the X chromosome in Drosophila became attached to one of the two large pairs or to the small IV chromosome, then the genes that were contained in the broken piece of X chromosome and that had formerly shown sex-linked inheritance would no longer do so. Likewise, if a piece of one of the autosomes was broken off and became attached to an X chromosome, these autosomal genes that had formerly shown ordinary Mendelian inheritance would now show sex-linked inheritance.

Such a case involving a block of autosomal genes in the II chromosome was discovered by Altenburg. This block of genes suddenly began to exhibit sex-linked inheritance as if it had become attached to an X chromosome. Cytological examination revealed the fact that one of the members of the II pair of large autosomal chromosomes was very much

reduced in size, whereas one of the X chromosomes had been increased in size by just about that amount. Many cases of translocation have been studied in recent years. They are generally first evidenced by peculiar genetic behavior and then checked cytologically, though the reverse of this process has been true in a few cases.

Reciprocal Translocations.—We learned earlier that during meiosis there might be an equal interchange of various-sized blocks of genes between nonsister, homologous chromatids. This process was called *crossing over*. So too, may there be interchanges of blocks of genes between two nonsister, nonhomologous chromatids or perhaps between nonhomologous chromosomes (illegitimate crossing over). This is called *reciprocal translocation*, or *segmental interchange*. In ordinary translocation there is no trading between the chromosomes or chromatids, a section of one chromosome simply going over to another chromosome without any reciprocity on the part of the latter. In reciprocal trans-

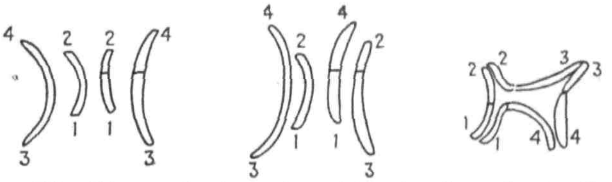

FIG. 105.—Diagram showing reciprocal translocation and catenation.

location, there is reciprocity, and it is between nonhomologous chromatids or chromosomes. This type of translocation happens more frequently than does simple translocation.

If there were reciprocal translocation between one end of the II and III chromosomes in Drosophila, then at synapsis, when like genes apparently attract each other to form the synaptic knot, a ring of chromosomes would be formed as indicated in Fig. 105.

These ring formations are known as *catenations*. Many peculiar synaptic configurations can be explained by means of reciprocal translocations, for the homologous parts of chromosomes apparently attract each other at synapsis. Chains and other queer formations of the chromatin material also result from the attraction of homologous parts of chromosomes that through reciprocal translocation have come to occupy abnormal places.

Since these abnormal formations of the chromosomes at synapsis are found in nature, many having been discovered by Blakeslee, Belling, and others in the Jimson weed (Datura), as well as being possible of creation by experimental treatment of plants through irradiation, it is assumed that they, along with all the other types of gene and chromosomal changes, are responsible for certain evolutionary changes. It has been

shown for instance that the F_1 hybrid between a North and a South American species of Datura shows two circular formations of four chromosomes each, together with eight synapsing pairs. Painter's discovery of a similar amount of chromatin material in the rat and the mouse, although differently arranged, has furnished the basis for the belief that these two species have arisen from a common ancestor through translocations and gene mutations.

The present wide complexity of the gene contents of the chromosomes must also be due in large measure to the translocations which have occurred in the past. For example, in Drosophila the numerous experiments have shown that genes producing reactions which control the same part of the body (such as the eye) may be located in different chromosomes. This may be due to ancient translocations which duplicated the genes for the particular character concerned. Later these would become differentiated from one another by changes in the genes, and we now find these similar genes in the different chromosomes all producing a reaction on the same part of the body. In this way the complexity of organisms must have been immensely increased, and it is evident that translocations giving rise to transmutations of chromosomes have played a great part in the general progress from lower to higher organisms which has taken place and they may be regarded as one of the prime factors in Creative Evolution.[1]

Inversion.—Another type of chromosomal mutation is that called *inversion.* In this situation a portion of a chromosome has in some

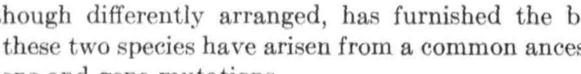

FIG. 106.—Diagram of process of inversion.

manner become inverted. This might happen because a chromosome became looped upon itself and then failed to uncoil in the normal manner. This possibility is indicated in Fig. 106.

An instance of inversion is found in Drosophila. There are two species of Drosophila (*melanogaster* and *simulans*) that are interfertile, although the hybrids are sterile. Chromosome maps for both species have been constructed from the data of breeding experiments and these show that the genes are very similarly located in the two species in chromosomes I and IV. In chromosome II the genes so far studied appear to be in the same order although there are variations in the distances between genes in the two species. In chromosome III not only are there differences in the distances between genes but in about the middle of the chromosome in *D. simulans* a section has become completely inverted in comparison with *D. melanogaster*.

[1] HURST, C. C., "The Mechanism of Creative Evolution," p. 81, The Macmillan Company, New York, 1932.

Deficiency.—Still another type of mutation is that known as *deficiency*. This arises from the loss or inactivation of a portion of chromosome, which is not lethal provided the deficiency is not too large and the organism is not homozygous for the deficiency. One of the best known examples of deficiency is that leading to the production of notched wings in Drosophila. Notch behaves as a dominant, is lethal when homozygous, and is located at about point 3 in the X chromosome.

A Notch female from a red-eyed stock crossed with a white male gives Notch and normal offspring as expected, but all the Notch flies show the recessive white eye (which is located at 1.5), as though the Notch female contained no wild-type allele of white. The normal-winged flies are all red-eyed. Similarly, the gene facet, at 3.0, showed this peculiar pseudodominance when crossed with Notch,

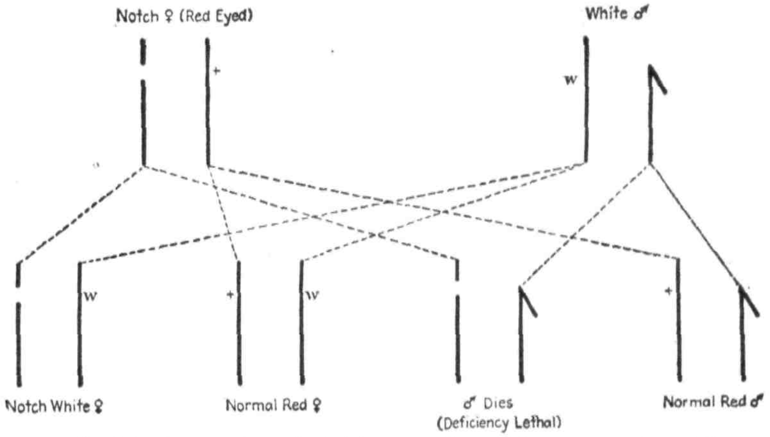

FIG. 107.—The inheritance of notch deficiency in *Drosophila melanogaster*. (*Sinnott and Dunn, Principles of Genetics.*)

and the gene Abnormal at 4.5 was also affected. Bridges and Mohr, who studied this condition, assumed that Notch was due to the absence of a piece of chromosome in this case bearing the loci from white through Abnormal. This was called a deficiency and in conformity with the assumption, the map of the X in Notch is about four units shorter than normal. Much later the actual absence of this section of the chromosome in Notch females was proved by examination of the salivary gland chromosome.[1]

Duplication.—We have seen in the previous section that a chromosome may become deficient or lacking in certain genes by a portion of a chromosome becoming lost. This might occur through unequal crossing over between two homologous chromosomes. If this happened, the unequal interchange, besides producing a deficient chromosome, would

[1] SINNOTT, EDMUND W., and DUNN, L. C., "Principles of Genetics," 3d ed., pp. 233–234, McGraw-Hill Book Company, Inc., New York, 1939.

also give rise to a chromosome with some genes duplicated. This is illustrated in Fig. 108.

One of the above chromosomes is deficient for genes *B* and *C*, whereas the other has a double dose of these genes, *i.e.*, they are duplicated.

A chromosome fragment, however it arises, is known as a *duplication*, and it may exist by itself or become attached to some other chromosome.

One of the best known duplications is that of the bar eye pattern in Drosophila, long known as a dominant at point 57 in the X chromosome. Zeleny found that homozygous bar-eyed flies very occasionally produced normal round-eyed offspring and even less frequently the ultra- or double-bar pattern. By the use of other mutant genes close to bar, Sturtevant and Morgan showed these exceptions to be due to unequal crossing over at the bar region, so that the normals showed a slight deficiency compared with bar and the double bar a duplication. Since the normal flies showed no actual deficiency, it was reasoned that bar was originally a duplication. These facts have been substantiated by Bridges' cytological study of the salivary-gland chromosomes, which shows bar to be a duplication. The further fact that the duplication in separate chromosomes produces bar, and that, when the duplication occurs in one chromosome, it produces double bar led Sturtevant to the conclusion that

FIG. 108.—Diagram illustrating both deficiency and duplication due to unequal crossing over.

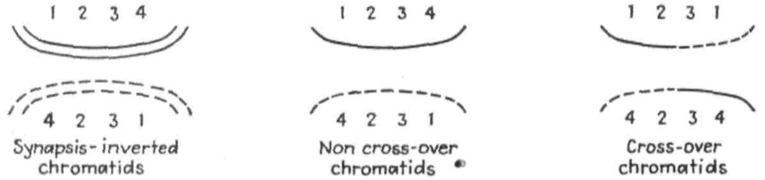

FIG. 109.—Diagram of duplications due to inversions.

the position of the gene in the chromosome, as well as its nature, was influencial in the final effect produced. This is the *position-effect* theory.

Duplications may also arise from crossing over between inverted portions of two chromosomes as illustrated in Fig. 109.

Heteroploidy.—A new organism generally arises from the union of an egg and a sperm in each of which the number of chromosomes has been reduced to the half or haploid number (n). The coming together of these two half numbers at fertilization again restores the chromosomes to the diploid number ($2n$). Sometimes a new organism gets one (rarely two) too many or one too few chromosomes and is therefore $2n + 1$ or

$2n - 1$. Many of these are viable and have been studied both genetically and cytologically. These individuals differ slightly from the wild type in appearance and are often less viable, less fertile, and do not breed true.

In Drosophila, forms are known that lack one member of the small IV pair of chromosomes. Such a fly with only one IV chromosome is called a *haplo*-IV fly, and one with an extra IV chromosome is called a *triplo*-IV fly. These individuals, with any greater or smaller number of chromosomes than the normal for the species, vary from the normal to a greater or less extent. In other words, the normal number of chromosomes is necessary for the production of a "normal" individual, though this does not mean that those individuals not having the normal number of chromosomes will necessarily be unable to survive and leave offspring.

Triplo-IV Drosophila have narrow, pointed wings, smooth eyes, course bristles. When crossed with eyeless, they give ½ triplos: ½ wild type. These triplo F_1 flies crossed back to eyeless give 5 wild type : 1 eyeless. Nondisjunction of the two X chromosomes, discovered by Bridges, produces another form of heteroploidy. White-eyed females crossed with red-eyed males should yield red-eyed females and white-eyed males but occasionally do just the opposite owing to nondisjunction of the X chromosomes following synapsis.

In the Jimson weed, which has 12 pairs of chromosomes, Blakeslee, Belling, and their coworkers have discovered many types of heteroploids. Any one chromosome present in a triple dose gives what is termed a *primary heteroploid*. All the possible 12 primaries have been studied, and each of them has a characteristic mutant appearance. Another type with the extra chromosome made up of parts of two homologous chromosomes rather than being just an additional whole chromosome is called a *secondary heteroploid*, and still another type with the extra chromosome made up of parts of two heterologous chromosomes is called a *tertiary heteroploid*. These latter two types give many peculiar ring formations of the chromosomes at synapsis.

In the evening primrose (Oenothera), in which the diploid number of chromosomes is 14, the following number of chromosomes, according to Gates, have been reported: 15, 20, 21, 23, 27, 28, 29, 30. Those with other than 14 chromosomes have definitely distinguishing somatic characters, which indicates again that the characters are under the control of the genes.

Haploidy.—The haploid condition is normal in some species that reproduce parthenogenetically, *e.g.*, bees, wasps, some moths, and rotifers. A few other species can be made to reproduce parthenogenetically by artificial means, *e.g.*, certain amphibians. This has recently been accomplished by Pincus in the rabbit with the probable

aa BB, and *aa bb* forms, or 2^2. With 15 pairs of genes, we would get 2^{15} different forms. Selfing is of course the closest sort of inbreeding possible. It should be noted that, granted equal viability, the number of recessive and dominant genes in the population remains the same.

Inbreeding, therefore, is seen to have a direct effect on variation. When it is practiced, the population tends to increase in variability by becoming broken up into many separate, though highly uniform, families or strains. This, of course, offers greater opportunities for selection within desirable uniform lines, and, when this sort of selection is practiced, the population becomes more uniform, owing to the selection, however, rather than the inbreeding.

In the higher animals, however, selfing is not possible because the union of an egg and a sperm produced by two separate individuals is necessary to produce a new individual. If we start with the animals *Aa* and *Aa* and their offspring interbreed freely, the population will

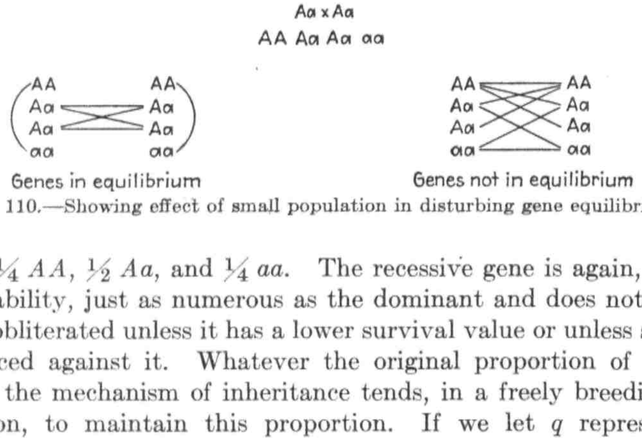

FIG. 110.—Showing effect of small population in disturbing gene equilibrium.

become ¼ *AA*, ½ *Aa*, and ¼ *aa*. The recessive gene is again, granted equal viability, just as numerous as the dominant and does not tend to become obliterated unless it has a lower survival value or unless selection is practiced against it. Whatever the original proportion of the two genes is, the mechanism of inheritance tends, in a freely breeding large population, to maintain this proportion. If we let q represent the original proportion of A, and $1 - q$ the original proportion of a, then in any succeeding generation the proportions of the homo- and heterozygotes will be $q^2\ AA : 2q(1 - q)\ Aa : (1 - q)^2\ aa$.

If we knew that 1 per cent of Holstein calves were the recessive red (*aa*), then we would also know that 81 per cent were homozygous black (*AA*) and 18 per cent heterozygous (*Aa*), because, if $(1 - q)^2 = 0.01$, then $(1 - q) = 0.1$, and, since the whole population is unity, or 1, then q must equal 0.9 and q^2 0.81 and $2q(1 - q) = 0.18$. If inbreeding were practiced in this population, the proportion of homozygotes would of course be increased at the expense of the heterozygotes.

The above discussion of genetic equilibrium applies only to very large populations. In small populations, however, the mechanism of inheritance tends to reduce variation by eliminating certain genes at the same

time that it is fixing others in a homozygous state. Thus, if we have two Aa parents and only 2 of their offspring can survive (limited population), then the likelihood that the genes will remain in equilibrium is less than the likelihood that there will be more of one kind than the other. This is shown diagrammatically in Fig. 110.

It will be seen from Fig. 110 that in small populations the tendency will be for the population to be made up of all A or a, the other gene being lost. Thus in small isolated populations there will be a tendency for differentiation into local races quite independent of natural selection.

Nicking.—If offspring of certain matings are of a high order of excellence and in general better than their parents, then breeders say they "nicked" well. It sometimes happens that the mating of two average animals results in the production of an outstanding individual from the standpoint of type, performance, or both. This effect may, of course, be largely due to environment. It may, on the other hand, be due to inheritance. Possibly each parent was lacking in certain genes that would make for excellence although possessing a great many of the necessary genes. If the two parents lacked in different genes, the offspring might get a full complement, some from each parent. Crosses of white-eyed and eyeless Drosophila result in normal red-eyed offspring. One parent is recessive for a pair of genes making the eyes white, though it has the normal genes for presence of eyes. The other parent is recessive for the genes for presence of eyes but has the normal genes for red eyes. When mated, each parent supplies what the other lacked, thus giving normal red eyes.

It must be remembered, however, that these offspring are heterozygous and cannot breed true. Sometimes the argument that geniuses do not always beget geniuses is used against the chromosomal theory of inheritance. If, however, the genius arose as did the red-eyed flies just mentioned, we would not necessarily expect him to beget geniuses, so that in place of refuting the theory of inheritance, facts such as these tend to substantiate it. When favorable "nicks" arise their breeding ability must receive careful scrutiny before they are approved, because it is possible that their diverse origins will be manifest in their offspring.

Prepotency.—The term *prepotency* is often used in rather a loose fashion and is applied generally to males. It is usually thought to be associated with the general characteristic of vigor. That is, it is applied very often to an outstandingly vigorous male. The term really means the ability of an animal, male or female, to stamp its own characteristics on its offspring. For instance, the Hereford bulls used on the grade cattle of the range generally put white faces on all the offspring of such matings. If a Hereford-Angus cross is made, however, a white-faced

black-bodied[1] polled individual is produced, and the question arises a to which animal is prepotent. Some will say the Hereford because c the white face on the offspring. Others will say the Angus because of th polled characteristic and black body. The truth is, however, that on is not justified in speaking of either animal as being prepotent. Th animal is not prepotent; the various characteristics that the animal ma: exhibit may or may not be prepotent. In this case, polledness of th Angus, white face of the Hereford, and black body color of the Angus i each prepotent. The same results would be secured no matter whicl one of the breeds in the above cross was selected as the male and whicl one as the female and also regardless of vigor. Graphically the result in regard to these three characters and with the dominant character italicized might be represented as follows:

PP polled	Angus	*pp* horned	Hereford
ww black face		*WW white face*	
BB black body		*bb* red body	

PwB pWb
PpWwBb
polled white-faced black-bodied crossbred

It is not enough, however, to say that certain characters are pre potent. When the above crossbred produces spermatozoa or ova, a: the case may be, the factors will separate and recombine into all th possible combinations, reduction taking place at the same time, so tha ova or spermatozoa of the following make-up are produced: *PWB PWb, PwB, Pwb, pWB, pwB, pWb, pwb.* If one of the above crossbred is mated to a Hereford pure for horns, white face, and red body, o *pp WW bb*, and hence capable of producing only *pWb* spermatozoa o ova, calves will result 50 per cent of which will be horned and 50 per cen of which will be red-bodied. Thus, the characters which are fully prepotent in the purebred, *viz.*, polledness and black body, cease to be fully prepotent in the crossbred, because the crossbred produces more than one kind of reproductive cell, actually producing eight differen kinds as to these three characteristics of horns, face color, and body color. The above characters are simple in their nature, being controlled specifically by one factor, although many other factors may be involved According to Wright:

Most characteristics probably depend on a large number of hereditary units, but nevertheless the nature of prepotency is believed to be essentially the same. So far as there is prepotency, it is a property of characteristics (or really of the

[1] The Angus might be heterozygous for color and therefore give rise to a red-bodied calf.

hereditary units back of the characteristics), not of individuals, breeds, or sexes, and whatever the characteristics, there can be no prepotency unless the individual produces only one kind of reproductive cell so far as it is concerned.

Technically, prepotency depends upon the character being dominant and the individual being homozygous; *i.e.*, the individual must carry *AA* in its chromosomes, not *Aa* or *aa*. The more prepotent an individual is, the less the probability of variation, good or bad.

A prepotent animal will have offspring that closely resemble it, but whether or not these offspring are themselves prepotent will depend on what genes they got from their other parent. If they have many homozygous dominant genes, they will be prepotent. An animal is seen, therefore, to be unable to transmit its own prepotency because it contributes but one-half of its total inheritance to any of its offspring.

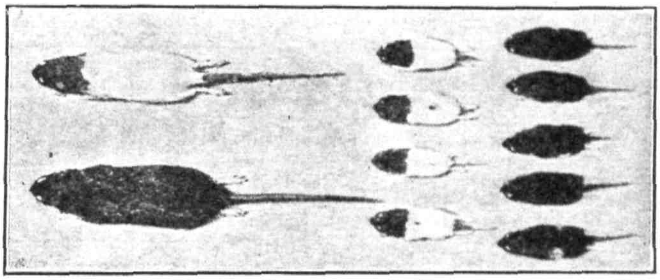

FIG. 111.—Inheritance of a recessive pattern of white spotting seen in "hooded" rats. The parents (at the left) are a homozygous hooded mother and a heterozygous "Irish" father (black with white belly). An entire litter of their young is shown at the right. Four are homozygous hooded like the mother, five are heterozygotes like the father. Note fluctuation in both classes. Such fluctuations are found to be in part heritable. (*From Castle, Genetics and Eugenics, Harvard University Press.*)

Variation Guided by Selection.—Although it may be questioned whether selecting animals with a definite end in view can specifically be said to cause variations in that direction, it is, nevertheless, true that one variation in a given direction seems to make other variations in that direction more probable. Thus it is well-known that by selecting in Holsteins or Ayrshires the proportion of pigmented to nonpigmented area may be shifted from one of almost entire pigmentation to one almost white. Likewise, in Herefords, the white of the face, which behaves as a unit in inheritance, may be increased or decreased in area. Functional variations, such as speed in horses, milk production in cattle, wool production in sheep, etc., can also be guided by selection—in fact, it has been selection, both natural and artificial, that has given rise to most varieties and perhaps species. Castle states as an interpretation of factorial behavior in such selection:

Many students of genetics at present regard unit-characters as unchangeable. They consider them as impossible of modification as are the atoms. To recall

Bateson's comparison, the carbon and oxygen of carbon monoxide, CO, are each unchangeable. Adding another atom of oxygen does not alter them, though it changes radically the compound formed which becomes carbon dioxide, CO_2, possessed of very different properties. But the carbon and the oxygen are still there, unaltered and recoverable. This question is one of great practical importance,—are unit-characters as constant as atoms, so that we can merely recombine them, or are they different in nature from atoms so that we can modify as well as recombine them. Much careful work has been devoted to the solution of this question. It was at first assumed from chemical analogy that characters which behave as units in heredity must, like C and O in the case of carbon dioxide, emerge from combinations unmodified. But presently case after case came to light in which this was not true. Albinism emerged from crosses tainted with color; clear yellows emerged from crosses intensified to red, or diluted to cream, or sooty with minute quantities of black; patterns such as are seen in Dutch or in English rabbits, or in hooded rats, emerged considerably altered in

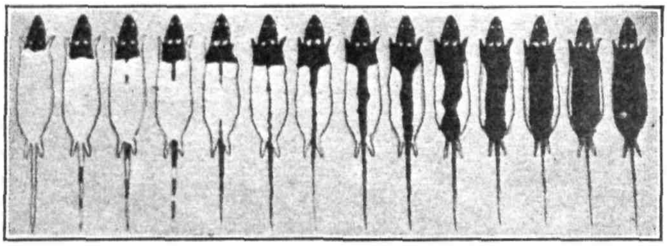

FIG. 112.—A series of grades for classifying the plus and minus variations of the white spotting pattern of hooded rats. (*From Castle, Genetics and Eugenics, Harvard University Press.*)

appearance. Facts such as these were interpreted in two different ways. It was assumed by some that the actual unit-character, factor, or gene involved was subject to quantitative and possibly to qualitative change. By others it was assumed that the observed character changes were not due to changes in single genes but to the supplemental or modifying action of the other genes.

Hooded Rats and Selection.—As a test of these rival interpretations, we may discuss a typical case. The hooded pattern of rats clearly behaves as a simple unit-character allelomorphic to Irish pattern or to self in crosses. But the hooded pattern as seen either in pure-bred or in cross-bred litters of young varies slightly, and such variations have a genetic basis since by selecting either the whitest or the blackest individuals, one can either whiten or blacken the average racial condition. Races corresponding with the extremes of the series shown in Fig. 112 were thus produced. The question now arose whether the observed changes had occurred as a result of change in the single unit-character or gene clearly concerned in the case, or whether this was due to other agencies. To test the matter the selected races, now modified genetically in opposite directions, were crossed repeatedly with a non-hooded (wild) race. The recessive hooded character disappeared in F_1 but was recovered again in F_2 in the expected 25 per cent of this generation. These extracted hooded individuals, following each cross, were

less divergent than their hooded grandparents from the ordinary hooded pattern. After three successive crosses (six generations) the whitest individuals extracted from the dark hooded race were no darker than the darkest individuals extracted from the white hooded race. In other words repeated crossing with the non-hooded (wild) race had caused the changes in the hooded character, which had been secured by selection, largely to disappear. The conclusion was drawn that the hooded allelomorph itself had remained unchanged throughout the selection experiment, and that the phenotype had been altered by associating with the hooded gene a different assortment of other genes in each of the selected races, these serving as genetic modifiers. In the course of the selection experiment a mutation was observed to occur in the plus series to practically the Irish stage. This is not included in the summary but is mentioned to show how it is possible for selection to be aided in its progress by the occurrence of contemporaneous genetic changes, no less than by the sorting out of variations originally present in the foundation stock. Apart from the mutation mentioned the results of selection in this case show conclusively that the changes obtained had not occurred in the gene for the hooded pattern, but in the residual heredity. Other cases of apparent gradual change in unit-characters under the action of selection may be explained in a similar way. Accordingly, we are led to conclude that unit-characters or genes are remarkably constant and that when they seem to change as a result of hybridization or of selection unattended by hybridization, the changes are rather in the total complex of factors concerned in heredity than in single genes.[1]

Types and Frequency of Variation.—All animals will produce variations to a greater or less degree, depending upon the interaction of a great many factors. Sometimes extremely valuable animals arise from the mating of mediocre parents. Such variates should be studied carefully as to their ability to transmit their own desirable features, and nothing along this line should be taken for granted. Of decidedly more value than the animal that produces one such outstanding individual and a host of inferior ones is the animal that has a tendency to beget a uniform lot of offspring better than the preceding generation, even if the increase in excellence is small in each individual.

Innumerable instances could be cited of full brothers that are evidently genetically unlike, because their offspring are very unlike. The same is true of full sisters; *e.g.*, in cattle, one sister is often vastly superior to another in milk production. It is quite evident, therefore, that variation is a very potent and ever-present force molding new forms both anatomically and physiologically, and that its mechanism is to be sought in the genes and chromosomes, their interactions with each other, and their potentiality for individual change.

[1] Castle, W. E., "Genetics and Eugenics," pp. 237–240, Harvard University Press, Cambridge, Mass., 1930. (Reprinted by permission of the President and Fellows of Harvard College.)

Summary.—We have seen in this chapter that the genes and chromosomes may undergo a great variety of changes. As we would expect, such gene or chromosomal changes tend to be hereditary, for the genes and chromosomes are the actual mechanism of inheritance. The breeders' raw material for fashioning finer animals is variation. He must determine what the cause of the variation is and so plan his breeding operations to conserve the good and weed out the bad variations. He does this largely by selection and systems of breeding. Genetic variation is a complex mechanism and is made more difficult by the effects of various types of dominance and epistasis as well as by the fact that most characters are more or less elastic under different environmental influences. An understanding of the underlying mechanism of variation makes us more cognizant of the inherent difficulties involved as well as more confident of ultimate success when our understanding of principles is fully mature.

References[1]

[1] See lists at end of Chaps. XII and XIII.

CHAPTER XVII

THE PRINCIPLES OF VARIATION (*Continued*)

As stated in the previous chapter, there are two sorts of variation, genetic and somatic. We have seen that any changes in the genes or chromosomes may be inherited, because the genes and chromosomes from the parents form the actual "bridge of inheritance" between any individual and all of its millions of ancestors. We also learned that variations might be due to internal or to external stimuli. In this chapter we shall be concerned primarily with somatic variations that are generally caused by external stimuli, or, in other words, by the environment.

It seems almost certain that early in the evolutionary process the environment must have wielded a marked influence on the simple forms of life and caused their germ plasms to vary in different ways. Experimentally, this is possible in plants and lower animal forms today. In the higher animals, however, with their various adaptations for protecting the delicate germ cells, the possibility or extent of such external influences is much lessened. Parallel induction (same influence affecting both soma- and germ plasm) in the cases of alcohol or lead poisoning must be admitted, but here the effect appears to be temporary.

Environment and Somatic Variation.—Among the effective external stimuli are light, temperature, food, moisture, and other influences tending to make the organism deviate from its normal as specified by the make-up of the germ plasm that gave rise to it. As pointed out by Babcock and Clausen, external stimuli may affect the development of characters in three ways.

1. They may modify the development of inherited characters; *e.g.*, red, white, or blue light causes marked variations in the showy Sedum, even though the several plants be of the same genetic make-up. Temperature affects the degree of pigmentation in moths and butterflies. Food supply affects the relative size of body parts of Hyalodophina, a crustacean. Moisture affects the plumage color of pigeons.

2. They actually condition the production of characters whose hereditary determiners are present in the germ plasm. For example, light conditions normal development in plants. Temperature, when low, causes red flowers in the Chinese primrose, when high, induces white flowers. The kind of food supplied to the larvae of bees determines

whether the females shall be fertile (queen bees) or infertile (workers). Moisture concentration brings about development of abnormalities in black banding on the abdomen of Drosophila, a fruit fly.

3. They may cause germinal variations that result in the appearance of new heritable characters.

Modifications may be impressed on the soma from the outside; genetic variations are expressed from the inside, specifically from the germ plasm. The latter are heritable, whereas modifications seem to be nonheritable. If it is possible to modify the function of any organism in a given way, it must be because the organism inherited the ability to react in such a way. This does not necessarily mean that offspring from such an individual would necessarily show the same aptitude to modification. That would depend on the genetic make-up of the individual in question. The possible effect of amphimixis, or the bringing together of two diverse bits of germ plasm, must also be taken into consideration. Animals of a good strain that are themselves stunted and not developed to the limit of their inherent capacities may beget offspring of a type capable of great development. Daughters of scrub cows, developed under an environment tending toward full development of capabilities, produced 13 per cent more milk and 12 per cent more butterfat than their scrub dams of the same type of breeding, which had been developed under less favorable conditions.

It is the province of animal breeders to develop fully all the capabilities that their animals possess. Not that these so-called "modifications" will necessarily be inherited, but, if the parents exhibit favorable modifications, it must be because they carry that particular type of germ plasm, and, unless they are extremely heterozygous or amphimixis interferes, the offspring of such parents should in general exhibit like capabilities. Modification is an aid to selection but like all other aids must subject itself to the breeding test.

Acquired Characters.—The inheritance of acquired characters has been called "one of the historic battle grounds of biology." The animal breeder is vitally interested in the solution of the question of the inheritance of acquired characters. The successful breeder seeks to develop for himself and to leave to posterity a better type of animal than the one with which he was supplied at the beginning. It is perfectly natural for him to hope, and perhaps believe, that any increase in quantity or quality of produce he can bring about will be cumulative in his animals.

Before proceeding to a discussion of the evidence pro and con, it is essential to define specifically what is meant by an acquired character. Shull defines acquired characters as "those modifications of bodily structure or habit which are impressed upon the organism during its individual life." As Thompson has stated it, the precise question at

issue is this: "Can a structural change in the body, induced by some change in use or disuse or by a change in surrounding influence, affect the germ cells in such a specific or representative way that the offspring will through its inheritance exhibit, even in a slight degree, the modifications which the parent acquired?"

Any one of the higher organisms is the result of the union of a certain spermatozoon with a certain ovum. The chromosomal content of the particular spermatozoon and of the ovum that have united to produce any given individual determines the normal characteristics for this individual. With normal nutriment and a normal environment the individual will approximate its own norm as specified through its inheritance. Now both the anatomy and physiology of the organism are perfectly capable of modification, and the precise question at issue is whether or not such bodily modifications will be impressed upon the germ cells and thus become a part of inheritance.

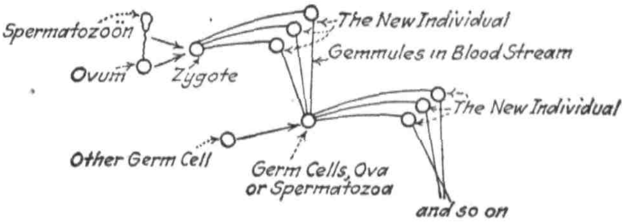

FIG. 113.—Schematic representation of the supposed method of transmission of acquired characters.

In an evolutionary sense all the characteristics that present-day organisms exhibit have been acquired, for evolution teaches that life originated in a very simple form and that it has gradually grown more complex—in other words, has ever continued to evidence new characteristics. Even this, however, is far from proof that changes in the somatic cells caused changes in the germ cells. May not the reverse of the last statement be the truth of the matter? Aligning cause and effect into their true relationship is not always an easy thing to do.

Lamarckism vs. Weismannism.—Lamarck, a French scientist, and Darwin, the famous English author of "The Origin of Species," believed that acquired characters could be inherited, and for a mechanism it was postulated that the blood stream which bathes all parts of the body would have something (gemmules) put into it by the part affected or by the character acquired and that the blood, later flowing to testicles and ovaries, would deposit this something in the ova or spermatozoa and thus bring about the development of the character in the offspring. This is the theory of pangenesis.

Weismann has been the chief antagonist of the theory of the inheritance of acquired characters, and he also developed the idea of the con-

tinuity of the germ plasm. Under this conception the germ cells that any individual produces are thought of as arising, as do all the other cells of this individual, from the original zygote. Under this view the type of germ cell produced is dependent on the nature of the original zygote and is not affected by the soma or body that has also arisen from the original zygote. The accompanying diagrams should make clear the differing features of these two systems.

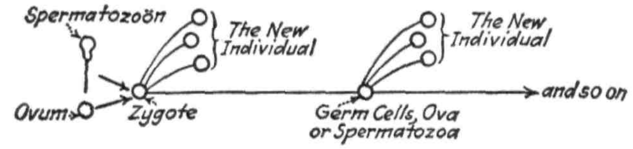

FIG. 114.—Schematic representation of the continuity of the germplasm. The drawing also illustrates the fact that germ cells arise from previous germ cells rather than from present somatoplasm.

Requirements for Proof of Inheritance of Acquired Characters.—Babcock and Clausen say:

To satisfy the rigid requirements of an experimental proof any evidence of the inheritance of acquired characters must fulfill the following conditions:

First, a specific character or modification in the body or soma must be impressed upon the organism by a known factor in its environment or in its exercise of bodily function.

Second, the character or modification must be new. There must be no question of the reappearance of ancestral traits or characters, or of the specific relation of the determining factor to the character or modification in question.

Finally, the induced change in the organism must reappear to some, though not necessarily to its full degree in succeeding generations in the absence of the original factor which determined its production. Other conditions in the life of an offspring must remain unchanged.

The problem of the inheritance of acquired characters can be conveniently divided into the five following categories: (1) anatomical modifications, (2) environmental modifications, (3) functional modifications, (4) pathological modifications, and (5) psychological modifications.

Anatomical Modifications.—There are abundant data relating to mutilations. When the tail of a sheep is docked the sheep has acquired a character during its individual development, *viz.*, taillessness. It is also recognized at once that this characteristic is not passed on to descendants of this sheep, but in succeeding generations it will be necessary to dock the lambs notwithstanding the fact that docking has been practiced for hundreds or thousands of generations. In this category come also the clipping of the horns of cattle, docking of horses' tails, clipping of dogs' ears and tails, etc. In none of these cases is the acquired character continued in the offspring. In the human family, there might be mentioned

circumcision, which has been practiced for thousands of years, and also the binding of feet to prevent their full development practiced by Chinese women. Here, no more than in the cases cited of farm animals, is there found evidence that these acquired characters are being inherited in even the slightest degree.

Weismann in order to test this hypothesis cut off the tails of mice for 19 generations in succession and secured no shortening of the tails or absence of tails in any of the descendants. As Walter remarks: "It is a good thing that children of warriors do not inherit their parents' honorable scars of battle else we would have long since been a race of cripples." The same author also remarks in this regard that "evidently wooden legs are not inherited but wooden heads are."

Environmental Modifications.—The second category is that of environmental effects. Examples from both the plant and animal kingdoms can be cited. Capsella, a wayside weed, has gradually climbed to a mountainous habitat. As it climbed it "acquired" a dwarf character—at least it grows luxuriantly in the valley and is small, compact, and dwarfed in its mountain home, and, when taken back to the valley, continues in its dwarf characteristics. This can just as well, if not more logically, be explained by saying that those plants germinally constituted so that they grew somewhat dwarf would, for that reason, have a better chance of surviving under the more rigorous conditions and decreased food supply that prevail in an ever increasing degree as the mountains are ascended. In other words, the force bringing about the change was not the inheritance of acquired characters, but "natural selection," which no doubt always has and always will, provided man does not interfere, weed out those types and individuals poorly fitted for their environment and preserve and prosper those better fitted to survive under the existing conditions.

Another example is the wind-lashed trees of our sea coasts, with all the branches growing out on the land side and pointing landward, but it is not known that seed from such trees would produce trees with that peculiar habit of growth if the trees were grown where the almost steady sea breezes did not blow. The case of the persistent sunburn of white men long resident in India might also be mentioned, but this "acquired characteristic" fails to reappear in their children born in England.

Ponies inhabiting the Shetland Islands are dwarfed because of the harsh climatic conditions and resultant scanty food supply. If brought to America's corn belt, such animals would no doubt give rise to offspring that would greatly excel them in size. Now, if these larger offspring, after reaching maturity, are returned to the Shetland Islands, will they continue to produce offspring that will attain large size? It is very unlikely that they will, and, even though they did, natural selection would give as

logical and perhaps a more reasonable explanation than the inheritance of acquired characters could muster.

Functional Modifications.—The third category relates to inheritance of functional modifications due to use and disuse of parts. From a practical standpoint, along with the inheritance of disease, this probably furnishes the most interesting phase of the subject. It will be well at this point to examine critically just what is meant by acquired characters. Is the term more or less a misnomer? If so, would it not account for much of the loose thinking and arguing over the much-debated question? As Davenport suggests, the differences between animals in a given species are differences of degree and not of kind—they are quantitative and not qualitative. Horses show horse characteristics and not rabbit characteristics, except as both have certain general characteristics in common; cattle show characteristics of the cattle family and not those of the swine family, except as they have certain ones in common. Horses have draft power or speed, cattle give milk, hogs lay on fat—some, of course, to a greater degree than others—but they all exhibit the characteristics of their species and not the particular characteristics of other species. In other words, they inherit in the germ plasm all the potentialities of their species in greater or less degree, depending upon the strain to which they belong. In addition, the environment in which they develop and live determines how far these potentialities are developed. Therefore, if a horse is able to trot fast because of his having inherited the tendency and because the tendency has been given play for full development by a fast track, careful trainer, proper harness, etc., or if a cow inherited the tendency to produce large quantities of milk and this proclivity is subsequently fully developed by proper care, feeding, and management, is the assumption at all justified that these animals have acquired any new characteristics? The fair answer is that no new characteristics have been acquired by either the horse or the cow. Inherent characters have been developed, perhaps exceedingly well developed, but no new ones have been acquired.

The point at issue is whether or not any increased functional activity will be registered in the germ cells and thus influence future offspring. Under this heading Redfield's theory of "dynamic" evolution can be discussed. This is the belief that the exercise of any organ or function results in a corresponding storage of energy in the germ cells, such that the effects are transmitted to the next generation—in other words, that these "acquired characters" are transmitted. This theory would postulate that, if a cow were developed from an 8,000-lb. two-year-old into a 16,000-lb. ten-year-old, the calf produced in her tenth year would be a much higher milk producer than the one produced when she was two years old, owing to the cumulative effect of the increased production she had

attained, the same bull having been used to sire both heifers. This has a distinct practical bearing in all classes of livestock.

In his work to try to prove the existence of the inheritance of this acquired character or development in fast horses, Redfield first computed the average age of the immediate sires of the first 1,000 stallions taken alphabetically from the American Trotting Register, which he found to be 9.43 years. He then computed the average age of all the sires, four generations back, of the entire class of 2.10 trotters, a faster class than that dealt with previously, the upper limit for admission to the register being 2.30, and this average he found to be 13 years. From this material, he concluded that the 2.10 class was faster than the group first considered because their sires had gradually grown more speedy as they increased in age up to thirteen and that they had transmitted this dynamic development to their offspring.

Marshall critically points out the following shortcomings in Redfield's work. In the first place, he took in one case the immediate sire and, in the second case, all the sires included in the four-generation pedigrees. Marshall reminds us also that these four generations carry us back over the formative period of the trotting horse to the time of Hambletonian 10, who was himself a great sire of speed and left many sons and grandsons which, bred to faster mares, were even better sires of speed than he. Taking only the immediate sires of the 2.10 list, as was done with the first list of sires, Marshall finds the average to be 9.41 years, nearly the same figure Redfield secured for the first group, 9.43, and evidencing no advantage of the old sire over the young one.

In this matter of increased speed in succeeding generations of horses, it has not been proved that functional modifications have not been continued in the next generation, though it is a biased mind which would attribute all increase in speed to this factor and fail to recognize possibilities in amphimixis, possible mutations, better environmental influences, better harness and training methods, faster tracks, more skilled drivers, etc. Also, as has been suggested previously, is it not more likely that the germ cells caused the somatic changes rather than that the soma caused the germinal changes?

There is no conclusive scientific evidence in support of the inheritance of "acquired characters" regarding functional modifications or use and disuse of parts. This fact, however, should not influence breeders to decrease their efforts to provide the most favorable environment and to attain the fullest development of their breeding stock. Whether or not functional modifications are inherited, breeders should still seek the germ plasm carrying the greatest possibilities for high-class production and should seek, when offspring come from such germ plasm, to place it in the best environment and supply the best possible feeding and

management in order that its inherent capabilities may be developed to the fullest extent. Not that one must believe that this acquired development will be transmitted, because there is no sure ground for any such belief, but it is desirable to know the horse of greatest speed, the cow of highest production, the meat animals with the greatest tendency to grow, and the sheep capable of the greatest production of high-quality wool and mutton, because, if in general "like does produce like," it is such germ plasm that should be used for increasing herds and flocks.

Pathological Modifications.—The fourth category, *viz.*, the inheritance of disease is also a consideration of vast practical importance. It should be borne in mind that, from a scientific standpoint, the only thing that is inherited is the germ plasm, more particularly, the various factors carried in the chromosomes. From this standpoint it will readily be seen that there is no more true inheritance in the case of disease than there was in the case of functional development. The problem, however, like the latter, has a very practical bearing, and although it may be said that in neither case has the affirmative been proved, yet this lack of proof does not necessarily preclude the possibility of its existence. One of the commonly cited cases under this heading is that of tuberculosis. This, however, is clearly a case of reinfection in the offspring, abundant opportunity for which is furnished in the intimate relations between parent and offspring, though it is very possible and no doubt true that the tendency or susceptibility to the disease is inherited in the defective germ plasm from which have come both parent and offspring. It is well known that it is possible to produce healthy calves from tubercular cows and bulls, provided the calves are at once removed upon being born and taken to a clean barn—in other words, that the opportunity for the parents to reinfect the offspring is removed.

In this regard, it may be well to mention the factor of immunity to certain diseases that exists in different species and varieties. If, for instance, a husky Irish policeman and an anemic Jew employed in a sweat shop were both exposed to the same kind and intensity of tuberculosis, the husky policeman would be more liable to succumb to the disease, because, in the Jewish race, selection has established at least a partial immunity to this disease. The zebu is being crossed on the native cattle of Texas because of the former's relatively greater resistance to tick fever. The mulefoot hog is often claimed to be immune to cholera, though the claim has never been scientifically tested and substantiated.

The microscopic organisms causing various diseases, if present in the blood of a parent, may be carried to and deposited within the ovum before it is fertilized. Such organisms, although not part of the chromosomal material that alone is heritable, are carried in the same cell with it and will thus cause the disease to reappear in the offspring; in

other words, the reinfection may come either previous or subsequent to birth. The organisms causing pebrine in silk moths, Texas fever in cattle, and syphilis in man are of this type, but, as Walter says, the disease is no more inherited than a grain of sand placed within the ovum would be inherited, though, of course, for all practical purposes, it amounts to the same thing, as the offspring will suffer from the disease in question.

A very interesting study of disease susceptibility and resistance has been reported by Dr. L. C. Strong of St. Stephens College. The following quotation is taken from his paper:

My first experiment dealt with the inoculation of a malignant tissue (adenocarcinoma) subcutaneously into a series of hybrid mice of known relationship. Two original stocks of mice were employed. Every individual of the first stock (*dBr*) grew the transplant progressively; and every individual of the second stock (albino) proved to be resistant to the same tissue. By crossing these two distinct races of mice, a hybrid generation, known as the first filial generation, was produced, all the individuals of which reacted to the transplant as did the first original stock, that is, all the individuals grew the transplant progressively. By mating two individuals of this hybrid first filial generation together, a second filial generation was obtained that contained two classes of individuals as far as their physiological reaction to the same transplanted tissue was concerned. Three individuals out of every four obtained were like the original susceptible race and grew the tumor progressively; one out of every four individuals was negative like the second original albino non-susceptible race; a typical 3:1 ratio was obtained. This experiment demonstrates, therefore, that susceptibility to a transplantable tumor is dependent upon the same ultimate mechanism that the inheritance of eye pigmentation apparently is dependent on. A particular individual grows a transplanted tumor because there is present in its ultimate make-up at least a single germinal determiner for a special physiological function that was obtained from the zygote that gave rise to the individual.[1]

Roberts and Card have reported on a 10-year study of the inheritance of resistance to bacterial infection by *Salmonella pullorum* in chickens. Their summary and conclusions state:

From this experiment, ten years in duration and involving more than 29,000 birds, evidence has been obtained which clearly indicates that heredity is an important factor in resistance and susceptibility to infection with *Salmonella pullorum*. The existence of hereditary factors for resistance and susceptibility to pullorum disease is shown by the following results:

1. Selection was effective in producing strains of the domestic fowl more resistant than were unselected stocks in respect to infection by *Salmonella pullorum*.

2. The selected stocks were consistent in maintaining resistance through successive generations.

[1] STRONG, L. C., Inheritance of Cancer, *Jour. Hered.*, **15** (8): 355–360, 1934.

3. The F_1 generation produced by crossing resistant and susceptible stock was as resistant as the resistant parents.

4. Progeny of the F_1 individuals mated to resistant were significantly more resistant than were the progeny of the back-cross to susceptible.

5. In the F_2 generation susceptible and resistant strains were recovered by selection.

6. A susceptible male mated to susceptible females produced progeny which were much less resistant than were progeny of the same male mated to resistant females.

7. No significant difference was found between the progeny of susceptible and resistant females mated to the same resistant male.

8. Acquired immunity was not present in the experimental birds, the progeny of infected hens exhibiting no greater resistance to disease than the progeny of noninfected hens, infection and freedom from infection being determined by the agglutination test.

9. Resistance is dominant to susceptibility, but probably more than one gene is involved.

10. In an examination of the blood of noninoculated young chicks the number of erythrocytes was found to be greater in the resistant (6 out of 7 cases) than in the susceptible strain. The number of leucocytes was greater in the susceptible strain. The percentage of neutrophiles was lower in the resistant individuals (6 out of 7 cases). In inoculated chicks, the percentage of neutrophiles was much higher among the susceptibles at 6, 7, and 9 days than among inoculated resistant individuals of the same ages.[1]

Psychological Modifications.—Many people believe in the ordinary principles of inheritance as far as physical traits are concerned but balk at applying these same principles to mental traits. On the other hand, the belief that mental or artistic accomplishments are transmitted to one's offspring is particularly prevalent. True, if two parents develop artistic qualities their children are likely to be artistically inclined owing, however, to the fact that the parents had sets of genes which tended in this direction plus the very important additional fact that their children had a very favorable environment as far as the development of artistic qualities was concerned. Some experimental work with white rats (McDougall) has been interpreted as the inheritance of acquired learning of parent rats in choosing paths of escape after having been dropped into a tank of water. There appears to have been a more or less steady improvement in the succeeding generations of trained rats. In the fourteenth generation the best rat made 42 errors, the worst rat 102, with an average for all of 80. In the twenty-third generation the best rat made 3 errors, the worst 71, with an average of 25 errors for all. Even when reverse selection was practiced for two generations,

[1] ROBERTS, E., and CARD, L. E., 1935, Inheritance of Resistance to Bacterial Infection in Animals, *Ill. Agr. Expt. Sta. Bul.* 419. (Contains an excellent bibliography.)

improvement was evidenced. On its face, this looks like the inheritance of acquired learning. However, two important questions remain unanswered. Was the stock pure (homozygous) to start with? Was no selection, conscious or otherwise, practiced? Although the stock had been long inbred McDougall states that there were "very large individual differences between the animals in respect of the rate at which they master their tasks."

Tryon has shown that the assortive mating of bright with bright and dull with dull rats can lead to the separation into bright and dull strains of rats as far as running a maze is concerned.[1]

Griffith's work indicating the transmission of acquired disequilibration in rats has not been substantiated, whereas Pavlov himself withdrew his earlier claims for the transmission of acquired learning through conditioned reflexes in mice.

There is as yet no clean-cut proof that acquired psychological modifications are inherited by the offspring. Because grammar schools have been in existence for several hundred years one is tempted to ask, somewhat facetiously, why our present children do not enter high school or college rather than grammar school at the age of six, if the learning of their ancestors actually became part of the hereditary material.

Arguments against Inheritance of Acquired Characters.—The reasons for the general unwillingness to subscribe to the belief in the inheritance of acquired characters may be grouped as follows:

1. There is no known mechanism in the body capable of impressing soma or body changes on the germ cells.
2. The evidence, although considerable in some cases, is by no means conclusive.
3. The theories of the continuity of the germ plasm and of germinal variation can account sufficiently well for all observed facts of heredity.

In order to study the effect of the soma on the germ cells, Dr. Castle at Harvard removed the ovaries of a white guinea pig and substituted the ovaries of a black guinea pig. The operation was entirely successful, and in due time the animal was bred to a white male and produced in all three litters totaling 6 individuals. This female was white (with substituted black ovaries) and was bred to a white male. Albino bred to albino in guinea pig invariably produces white offspring, but in this case all the offspring were black. Some of these in later breeding trials behaved as normal black guinea pigs would be expected to behave. This critical experiment shows that the ova produced by those two black ovaries which had been transferred to a white body were, after a year's location in their new environment, still producing black ova,

[1] See SNYDER, L. H., "The Principle of Heredity," pp. 395–398, D. C. Heath and Company, Boston, 1940.

and it is indeed inconceivable that they could ever have produced any other kind. This experiment indicates that there is no mechanism in the body capable of impressing soma or body changes on the germ cells, though it, of course, does not prove this to be absolutely so, it being impossible to prove a universal negative.

Parallel Induction.—It is well known that the same thing may affect both soma and germplasm, *e.g.*, alcoholic or lead poisoning, etc., but this matter of the same thing affecting both does not come within the definition of an acquired character, which was that the modification must be first impressed upon the soma by a known factor in the environment or in use and disuse of parts, and the soma in turn must impress the modification on the germ cells.

Summary of Inheritance of Acquired Characters.—Castle gives the following summary on the inheritance of acquired characters:

The problem of acquired characters, after all, concerns only the higher animals. In the lower animals and in plants no such sharp distinction exists between body and germ-cells as we find in the higher animals. We may reproduce the entire plant from a cutting of root, stem, or even a leaf in some cases. Hence there is more chance in such cases of direct modification of the cells capable of reproduction, for most of the cells of the plant retain this capacity. In the lowest organisms (protozoa, bacteria) there is no distinction whatever between body and germ-cells. Every cell is capable of reproduction; and modifications produced in a cell by the environment are handed on directly to the next generation.

If in the lower organisms the potentialities of living substance can thus be altered, it seems reasonable to suppose that the same possibility may exist in the higher animals and plants, provided agencies capable of producing change are allowed to act on the germinal substance. It is the sheltered position of the germ-cells which seems ordinarily to exempt them from direct modification, but we cannot safely assume that they are in all cases free from such modification. Experiments of Stockard show that in guinea-pigs repeatedly intoxicated with alcohol, the germ-cells are enfeebled so that offspring of such parents, whether male or female, are more likely to be feeble and sickly, and so to die. Experiments of Hertwig show that similarly the germ-cells of frogs are capable of being injured by emanations of radium in consequence of which enfeebled or abnormal offspring may be produced.

Guyer and Smith have produced probably the best existing evidence for the artificial production of heritable defects. Injecting into the bodies of fowls the pulped lenses of rabbit eyes, they induced the production in the fowls' blood of antibodies which would neutralize harmful effects of the foreign material. Blood serum was then obtained from these immunized fowls and this serum was injected into the circulation of pregnant rabbits and made its way, it is thought, through the placenta into the circulation of the developing fetuses, where it interfered with the proper development of the eye in a certain number of embryos. Eye-defects such as opaque lenses, under-sized eyes, and eyes rotated out of their proper position, were thus obtained in two different and unrelated races of

rabbits. These defects reappeared sporadically among the inbred descendants of the abnormal rabbits, and so may be regarded as having become hereditary. Guyer and Smith consider the mode of inheritance that of a recessive Mendelian character, though fewer recessives are reported than theory demands; but this may be explained as due to the authors' failure to detect cases of slightly defective eyes, or to the failure of the character to find somatic expression in all cases.

In a third unrelated series of animals, Guyer and Smith injected pulped rabbit lens directly into the circulation of pregnant rabbits, and in this case also they obtained from one treated mother one young with defective eyes in a litter otherwise normal. The defect was transmitted in this case also.

The eye-defects in the experimental rabbits of Guyer and Smith were transmitted through male as well as through female parents. The authors believe that the antibodies artificially produced by the injected foreign bodies affected the constitution of germinal determiners at the same time that they affected corresponding somatic structures in the same individuals. In other words they favor "parallel induction" as an explanation of their results.

Finlay (1924) has repeated on mice the experiments of Guyer and Smith on rabbits, but with wholly negative results. He used rat lens, sheep lens, and ox lens to produce antibodies in pregnant mice, but without observing any eye-defects in the young of either the F_1 or the F_2 generations.

On the other hand, Little and Bagg, by X-raying pregnant mice, obtained young with pronounced eye-defects which were apparently inherited in the next generation as recessive characters. Hansen, too, X-rayed rats in utero and obtained eye- and other defects but without studying their inheritance. Stockard had previously obtained similar eye-defects in guinea-pigs by exposing the mothers to alcohol fumes. Hansen and Stockard are agreed that a variety of harmful agencies acting during the embryonic development of a vertebrate may so interfere with the complicated process of development of the eye as to lead to defective end results. They regard the defective eyes of the rabbits of Guyer and Smith not as specific effects of lens antibodies, as those authors supposed, but as due to disturbed development, maintaining that like results can be produced by any other disturbing agency.

If the germ-cells are capable either directly or indirectly of modification by outside agencies, evolution guided by the environment must be in some measure at least a reality. The truth then lies neither in the extreme Lamarckian view that all acquired characters are inherited nor in the extreme Weismannian view, that no extraneous influences modify the germ-plasm, but somewhere in between.[1]

Practical Phase of Inheritance of Acquired Characters.—Breeders should continue to develop their animals to the utmost. If this development is cumulative from generation to generation, breeders will profit thereby. If not, they will at least be able to see which animals are inherently capable of responding in the fullest degree to a favorable

[1] Castle, W. E., "Genetics and Eugenics," pp. 87–90, Harvard University Press, Cambridge, Mass., 1930. (Reprinted by permission of the President and Fellows of Harvard College.)

environment, and then, through selection of these animals as breeding stock and through wise matings, they will be able to bring about a gradual improvement in the stock under their care.

Telegony.—Telegony may be illustrated by the more or less common belief that, after a female has borne young by a certain male, her subsequent offspring will show characteristics derived from the previous sire. The classic example is that of a mare which bore offspring by a quagga and later produced horse colts that showed some striping. Numerous attempts have been made to confirm this by crossing mares and zebras, but in all cases they have failed. The basic elements that determine the characters of any individual are the ovum and the spermatozoon uniting to produce it. Spermatozoa from this first service could not possibly live over a gestation period in the female organs of any higher species to fertilize the next egg, as they live for a very few days at the most. If this first offspring had any influence on other undeveloped eggs in the ovaries, it would come under the heading of the inheritance of acquired characters, for which there is no conclusive proof. Mumford and Hutchinson made investigations in the mule-breeding district of Missouri, where mares often bear mule and later horse colts, but could find nothing to substantiate telegony. In the light of present knowledge of inheritance, telegony has neither experimental nor theoretical basis.

Maternal Impressions.—Belief in maternal impressions assumes that what a pregnant mother may see, hear, or experience may influence her offspring. In general, this old belief can be repudiated also, because, as Marshall points out, if it worked, all calves born in the spring up north would tend to be white because the mothers have viewed a white landscape all winter, and, similarly, calves born in the fall would be green. There is no direct nerve connection between parent and offspring to afford means for transporting ideas. Animal experiments have all given negative results in this field. It is, indeed, a fortunate provision of nature that in the higher animals the embryo is so well-protected from all external influences. If maternal impressions were actually registered on the offspring, all types and races would have long ago become a hideous, conglomerate mess.

Atavism or Reversion.—These terms, meaning the reappearance of some ancestral trait or character after a skip of one or several generations, are often encountered in the older literature on animal breeding. Such reappearances were more or less mysterious before the physical basis of inheritance was understood. The birth of a red Angus when the past four generations have been black is known to be due to each parent supplying a gene for red. Recessives may be carried along, hidden by dominants, for any number of generations. Whenever two recessives come together, or, in other words, whenever the dominant gene is lacking,

the "atavistic" character will be evident. Atavism or reversion is the sudden reappearance of some ancestral trait, but there is nothing mysterious about it, for it is one of the normal manifestations of the hereditary mechanism.

Summary.—We have tried to indicate in this chapter that the environment does play a large part in variation. Any organism inherits a certain "norm" based upon the nature of the genetic content of egg and sperm that unite to produce it. This "norm" however, may be influenced by many internal or external factors. It is like any elastic material, dough or newly mixed concrete. Within limits it can be molded into different forms by the environment. However susceptible the somatic tissue may be to molding, there is no conclusive evidence that molding of the soma itself can have any influence on the germ cells. By regulating food intake, any parent could be one-third lighter or heavier in weight, but his children's actual weight would not thereby be directly influenced. If we want heavier children, we will naturally select as the parents those who most readily put on weight. Variation therefore can be a very useful tool in directing selection. The task of differentiating between environmental and hereditary variation and between the various types of the latter is not easy but on its accomplishment depends the breeder's ultimate success. Variation can indicate new and desirable gene combinations. Seeing, seizing, perpetuating, and amplifying these lie at the base of any breeder's progress.

References[1]

Davenport, E. 1907. "Principles of Breeding," Ginn and Company, Boston.

Kammerer, P. 1924. "The Inheritance of Acquired Characteristics," Liveright Publishing Corporation, New York.

[1] See lists at end of Chaps. XII and XIII.

CHAPTER XVIII

STATISTICAL ANALYSIS OF VARIATION

We have now concluded our discussion of the orthodox principles of heredity and variation. In the former we learned that some characters of our animals are qualitative; *i.e.*, our horses are black or gray or sorrel, etc.; our cows are polled or horned, etc.; our hogs have upstanding or lop ears, etc. Qualitative characters behave in inheritance as though they were determined by one or a few pairs of genes, and, therefore, when crosses are made between animals differing in some qualitative character, we get some uniform expression of the character in the F_1 and sharp segregation into easily recognizable classes in the F_2. We have also tried to point out as we have gone along that most of the commercially valuable characters of our livestock are not of this simple qualitative nature but, on the contrary, are of a quantitative nature and behave in inheritance as though they were determined by many pairs of genes.

If we bred Thoroughbred mares averaging 1,000 lb. in weight to a Belgian stallion weighing 2,200 lb., we would expect the offspring or F_1 to be intermediate in weight; if we made the F_2 of this cross, we would expect to get a range in weights from around 1,000 lb. on up toward 2,200 lb. Likewise, if we bred 200 cows ranging in production from 8,000 to 10,000 lb. of milk to a bull with a transmitting ability for 15,000 lb. of milk, we would expect to get a group of 100 females that varied somewhat in their production but would average to produce about 12,000 lb. of milk; and, if we produced a large F_2 population, we would expect an increase in variation, perhaps reaching or surpassing the original limits of 8,000 and 15,000 lb. In other words, characters such as weight, milk or wool production, rate of growth, etc. do not segregate into easily recognizable and distinct classes but show a more or less uniform gradation from lowest to highest. They are quantitative and are probably controlled by many pairs of genes rather than by one or a few pairs.

Quantitative inheritance was formerly spoken of as "blending" and was at first erroneously thought to be outside the pale of Mendelian inheritance. Nilsson-Ehle and East independently proposed the multiple-factor hypothesis to explain this type of inheritance. It assumes that many pairs of genes scattered throughout the chromosomes act in an

additive or cumulative manner in bringing the character to expression. This theory has been amply demonstrated for many plant characters and forms the basis for the proving of sires, the most valuable technique for animal improvement now known.

It is a commonplace that animals differ in appearance or performance or both, and we have seen in the last two chapters that these differences may be caused by changes in genes or chromosomes or may be due to the environment or both. Our cows vary in milk production from 3,000 or 4,000 lb. a year to 40,000 lb. a year and in butterfat test from 2.5 to 7 or 8 per cent; draft horses vary in weight from 1,000 to 1,100 lb. to 2,000 to 2,500 lb.; and our meat animals show wide variations in rate of gain and grade of finished carcass. These qualities form graded series from smallest to largest or from poorest to best, *i.e.*, are quantitative and are therefore subject to mathematical analysis. In fact, it is only after they have been run through the mathematical mill that large masses of data can be made intelligible.

In order to arrive at a just estimate of the underlying facts, we must, of course, deal with relatively large samples of the populations under consideration. Comparing any one Percheron horse with any one Belgian or any single Jersey cow with any single Holstein cow could not give a just estimate of the differences between these breeds, whereas the comparison of the statistics of several randomly chosen animals of each breed can furnish the basis for a fair estimate, but only after the mass of data has been subjected to mathematical treatment. This statistical study of variation is called *biometry*.

It has been developed and is utilized to secure a numerical expression of differences and resemblances and to make comparisons of the results obtained. Because quantitative characters do blend and form graded series rather than independently recognizable classes, an elementary knowledge of biometry is essential for a proper understanding of the genetic principles involved in such inheritance. Biometry deals with variations, the kind of variations being of prime importance. There are two kinds that may approximate the normal variability curve, *viz.*, those due to recombinations of genetic factors and those due to environmental stimuli. If it is intended to study the workings of inherited characteristics, it will be essential to have very uniform external conditions, whereas, if it is desired to study environmental effects, it will be essential to approach a genetically pure line that is not varying because of recombinations of genetic factors.

If we use rams that shear 20 to 22 lb. of wool on ewes that shear 6 to 8 lb. of wool, we expect to get offspring that shear about 14 lb. of wool on the average and an F_2 population that still averages about 14 lb. but with a wider range of variability than that found in the F_1.

Pounds of Wool

Ewes		Rams
6, 7, 8		20, 21, 22
F_1 offspring	11, 12, 13, 14, 15, 16, 17, 18	
F_2 offspring	7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21	

Fig. 115.—Schematic cross of high and low wool production through F_2.

In the above schematic cross, we are assuming that many pairs of genes contribute to the production of a heavy fleece and that the rams have more of these genes than the original ewes. Because probably none of our animals is homozygous, however, the offspring of such matings would get different combinations of genes from their parents. We might assume in the above hypothetical case that there were genes (H) which determined 2 lb. of wool production and others (h) which determined $\frac{1}{4}$ lb. of wool production. If we assumed 14 genes determining wool production, then our ewes would have 2 H genes for the larger production and 12 h genes for the smaller, or $2 \times 2 = 4 + 12 \times \frac{1}{4} = 3$, or a total wool clip of 7 lb. Likewise the rams would have 10 H genes for the higher production and 4 h genes for the lower, or

$$10 \times 2 = 20 + 4 \times \tfrac{1}{4} = 1$$

or a total clip of 21 lb.

Ewes	Rams
Hh	*HH*
Hh	*HH*
hh	*HH*
hh	*Hh*
hh	*Hh*
hh	*Hh*
hh	*Hh*

The ewes would most usually pass along 6 h and 1 H gene, thus contributing $3\frac{1}{2}$ lb. to their offspring; whereas the rams would most usually pass along 5 H genes and 2 h genes, thus contributing $10\frac{1}{2}$ lb. to the offspring and giving many of the offspring a total wool production of 14 lb. The best the ram could contribute would be 7 H genes, or 14 lb.; the worst 3 H and 4 h, or 7 lb. The best the ewe could contribute would be 2 H and 5 h or $5\frac{1}{4}$ lb., and the worst 7 h or $1\frac{3}{4}$ lb., so that the offspring would range from $8\frac{3}{4}$ to $19\frac{1}{4}$ lb. of wool. Most of them would be at the 13-, 14-, and 15-lb. levels, a few at 12 and 16, fewer still at 11 and 17, etc. to the extreme limits. In the F_2, there would be the possibility of exceeding either the lower or the higher levels of the original parents, but with the average remaining at about 14 lb.

No one knows whether there are 14 or 140 genes concerned with wool production, and we all realize too that wool production is greatly influenced by feed, weather, and other environmental conditions. The above

example is entirely schematic and is used merely to try to tie up genetics and practical breeding problems with the rest of this chapter dealing with the statistical analysis of variation.

As an actual example of the workings of the laws of chance in yielding a normal distribution or dispersion of combinations, we might flip coins. If we flip a penny it may fall head or tail and the chance of its doing so is 1:1 or there is $\frac{1}{2}$ chance for each.

If we flip two coins simultaneously, they may both fall heads and will in $\frac{1}{2} \times \frac{1}{2}$, or $\frac{1}{4}$, of the flips, and the same for tails; whereas there are two ways of getting a head and a tail ($\frac{1}{2} \times \frac{1}{2}$, or $\frac{1}{4}$), so that $\frac{1}{2}$ of the flips would give one head and one tail.

If we flip three coins simultaneously, we expect to get three heads—$\frac{1}{2} \times \frac{1}{2} \times \frac{1}{2}$, or $\frac{1}{8}$ of the time; two heads and one tail—

$$\tfrac{1}{2} \times \tfrac{1}{2} \times \tfrac{1}{2} \times 3,$$

or $\frac{3}{8}$ of the time; two tails and one head—$\frac{1}{2} \times \frac{1}{2} \times \frac{1}{2} \times 3$, or $\frac{3}{8}$ of the time; and three tails—$\frac{1}{2} \times \frac{1}{2} \times \frac{1}{2}$, or $\frac{1}{8}$ of the time.

If we flip six coins simultaneously, we expect to get all heads on very rare occasions, actually $\frac{1}{2} \times \frac{1}{2} \times \frac{1}{2} \times \frac{1}{2} \times \frac{1}{2} \times \frac{1}{2}$, or 1:64 times. The probability of getting five heads and one tail, four heads and two tails, etc., is given by the ratio of coefficients of the various terms in the expansion of the bionomial $(a + b)^6$ to their sum, which are

$$1a^6 + 6a^5b + 15a^4b^2 + 20a^3b^3 + 15a^2b^4 + 6ab^5 + 1b^6$$

This begins to look quite similar to the dispersion of wool clip in our hypothetical data of Fig. 115, where we would expect to get a few sheep with low wool production, a few with high wool production, but most of them ranging close to the average wool production of their diverse parents.

Statistical Regularity.—The employment of the biometrical method makes it necessary to measure, weigh, or make other arbitrary classifications of the material at hand to compute the results and from them to draw general conclusions. It is possible to do this because of the law of statistical regularity, *viz.*, that a reasonably large amount of data picked at random from the mass, with no influences at work tending to make the choice vary in any specific direction, will give a sample, the average of which will be almost identical with the average of the whole; or, as stated by Weld, "If a number of different events are equally possible as regards constant conditions (that is, if there is no persistent reason why one should occur rather than another), and all are repeatedly given opportunity to occur, they will in the long run occur with equal average frequency."

Or as stated by King, "A moderately large number of items chosen at random from among a very large group are almost sure, on the average, to have the characteristics of the large group."

When we have found the mean or average of a sample of observations, we can then determine how much each item varied from the mean; and, if we added up all these deviations from the mean and divided by the number of items being studied, we would have the average deviation of each item. Such a procedure gives equal weight to all the variations, small and large.

If we were shooting at a target it would take very good marksmanship to be able to come within 2 in. of the bull's eye. But to come within 1 in. would require marksmanship not twice as good but four times as good, because the area of a circle 2 in. in diameter is four times as large as the area of a circle with a diameter of 1 in., just as a square bounded by 1 in. on each side (1 sq. in.) is only one-fourth as large as one bounded by 2 in. on a side (4 sq. in.). The area of the square is increasing by the square of

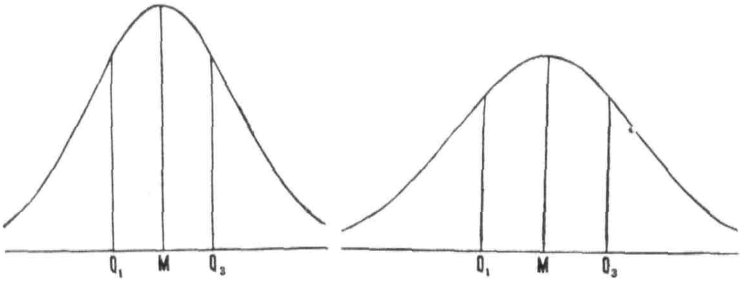

FIG. 117.—Two normal curves enclosing the same area but differing in the value of Q as as well as in range.

the measure of one of the equal sides, rather than just doubling as we go from a 1-in. square to a 2-in. square. For this reason the large variates from a mean (large misses from a target) are of more importance than the small ones. In order to give the large variates more influence and an influence mathematically in keeping with their importance, it is obvious that we should square all of the variates, and then, of course, at the end we must divide by the number of variates and extract the square root. When this is done, we have what is called the *standard deviation,* which is the most useful and most used measure of variation.

The older method of calculating the standard deviation (σ) used n as the divisor, but the mean is calculated from the total of the variates, and the algebraic sum of the deviations is zero, hence in n variates, when $n - 1$ deviations have already been calculated, the value of the final deviation is fixed, and there are, therefore, only $n - 1$ independent comparisons possible; *i.e.,* the *number of degrees of freedom* is $n - 1$. Because the mean square deviation should be evaluated from the number of independent comparisons of the variates with the mean, and there can only be $n - 1$ independent comparisons, this is a more accurate divisor

than n. The formula for the standard deviation (σ) is, therefore,

$$\sigma = \sqrt{\frac{\Sigma \text{ (each variate } - M)^2}{n - 1}}$$

Horse Height.—As an example to begin to show how statistics are used in studying variations, we will use the height of 30 Percheron horses. As is well-known, horses vary in height at the withers. Thirty Percherons were measured in this respect with the results indicated in Table 25.

TABLE 25.—HEIGHT OF HORSES

Horse number	Height in inches (y)	Deviation from mean ($y - M$) +	Deviation from mean ($y - M$) −	Square of deviation $(y - M)^2$
1	63	..	1	1
2	64	0	..	0
3	66	2	..	4
4	65	1	..	1
5	63	...	1	1
6	62	..	2	4
7	60	..	4	16
8	64	0	..	0
9	65	1	..	1
10	66	2	..	4
11	63	..	1	1
12	67	3	..	9
13	64	0	..	0
14	63	..	1	1
15	62	..	2	4
16	64	0	..	0
17	67	3	..	9
18	61	..	3	9
19	64	0	..	0
20	61	..	3	9
21	63	..	1	1
22	64	0	...	0
23	65	1	..	1
24	68	4	..	16
25	64	0	..	0
26	63	..	1	1
27	65	1	..	1
28	64	0	..	0
29	66	2	..	4
30	64	0	..	0
	30/1920	20	20	98
	64 in. = average height or mean (M)			

The mean or average height of these 30 horses is, therefore,

$$\frac{\text{Total height}}{n} = \frac{1{,}920}{30} = 64 \text{ in.}$$

The standard deviation of these variations from the average is

$$\sqrt{\frac{\Sigma\,(y - M)^2}{n - 1}} = \sqrt{\frac{98}{29}} = 1.83 \text{ in.}$$

The work involved in getting these results can be lessened by grouping the horses into classes according to height in a frequency table and by using a short method of calculation.

The Frequency Table.—Let us arrange these horses in their ascending order of height putting all those of the same height together into one group.

TABLE 26.—FREQUENCY TABLE OF HEIGHT MEASUREMENTS

Height of Horses, Inches	Frequency (Number in Each Class)
60	1
61	2
62	2
63	6
64	9
65	4
66	3
67	2
68	1
	30

The Frequency Graph.—Graphically, these data can be represented as shown in Fig. 118. The classes are indicated on the base line of coordinate paper and the frequencies plotted on the perpendicular.

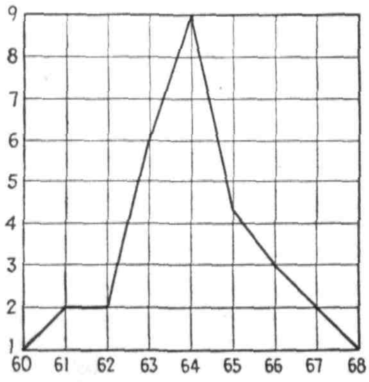

FIG. 118.—*Frequency graph of heights of horses.*

Figure 118 is the curve of these horse-height data. It simulates the normal curve of error but is not a smooth curve because there are too few entries and the class range (1 in.) is too large. If we took measurements of several hundred horses and measured to the ¼ in., our curve would, of course, be much smoother, would simulate the normal curve much more closely.

Mean by Short Method.—We have seen that the mean can be computed by adding together the heights of all the horses and dividing by n. We could also compute the mean by

multiplying each class in the frequency table (Table 26) by its respective frequency, summing these results and dividing by n.

In order to obviate the necessity of multiplying the values by the frequencies, a short method has been devised. In this a mean is assumed or guessed and the deviation of each class from this assumed mean is listed and the product of each class deviation times its frequency computed. These products are then added algebraically and divided by n to get the "correction for mean" to be added to the assumed mean in order to arrive at the correct value of the mean.

The assumed mean need not approximate the true mean and the lowest class is often assumed as the mean in order that all the deviations may be plus in sign. In our example we will take 63 in. as the assumed mean, M_a.

TABLE 27.—TO COMPUTE MEAN BY SHORT METHOD

Height of horses, y	Frequency, f	Deviations from assumed mean $(y - M_a)$	$f \cdot (y - M_a)$
60	1	−3	− 3
61	2	−2	− 4
62	2	−1	− 2
63	6	0	0
64	9	1	9
65	4	2	8
66	3	3	9
67	2	4	8
68	1	5	5
	$n = 30$		$\frac{+30}{n} = 1$

The sum of the class deviations (from assumed mean) times the respective frequencies gives an algebraic value of 30 for all the variates or 1 for each variate (n being 30). This is the "correction for mean" which must be added to our assumed mean in order to give us the correct mean.

$$\text{By short method } M = M_a + \frac{[\Sigma f \cdot (y - M_a)]}{n}$$

Standard Deviation—Short Method.—The standard deviation, which is preferred over the range, quartile, or average deviation as a measure of variation or dispersion because in computing it all the variates are squared, thus giving added weight to the extreme variates, may also be computed by the short method. The procedure involves squaring the

deviation $(y - M_a)$ of each class, multiplying by the respective class frequencies, summing, subtracting the correction factor

$$\text{C.F.} = \frac{[\Sigma f \cdot (y - M_a)]^2}{n}$$

dividing by $n - 1$, and extracting the square root as indicated in Table 28.

TABLE 28.—TO COMPUTE STANDARD DEVIATION BY SHORT METHOD

Height of horses	Frequency	Deviations from assumed mean $(y - M_a)$	$f \cdot (y - M_a)$	$f \cdot (y - M_a)^2$
60	1	−3	− 3	9
61	2	−2	− 4	8
62	2	−1	− 2	2
63	6	0		
64	9	1	9	9
65	4	2	8	16
66	3	3	9	27
67	2	4	8	32
68	1	5	5	25
			+30	128

$$\text{Short method } \sigma = \sqrt{\frac{\Sigma f \cdot (y - M_a)^2 - \text{C.F.}}{n - 1}}$$

$$\sigma = \sqrt{3.37}$$

$\sigma = 1.83$ as previously determined by the long method.

The sum of the squared deviations times their frequencies,

$$f \cdot (y - M_a)^2,$$

is called the sum of the squares or S.S. The square of the standard deviation, σ^2, is called the variance.

Coefficient of Variation.—Inasmuch as it is sometimes desired to compare results secured in different years or even to compare things measured in different units, it is necessary to have an expression that will make it possible to have a reliable measure of such variations. This is the coefficient of variation (C), and the formula for finding it is $\frac{\sigma \times 100}{M}$. In the case that has been under consideration the coefficient of variation is

$$C = \frac{1.83 \times 100}{64} = 2.86\%$$

If the standard deviation is large and the mean is small, the coefficient of variation will be large. This indicates that the plotted curve of the materials would be a wide flat one. If the standard deviation is small and the mean large, the coefficient of variation will be small, thus indicating a tall, narrow curve.

Probability.—In mathematics *probability* is expressed as the ratio of the number of times an event happens to the total number of trials made. Since a penny when flipped must fall either heads or tails; *i.e.*, there is an even chance (1:1) that it will fall either way, we would expect about 500 heads out of 1,000 tossings; in other words, the probability is 500:1,000 or ½ or 0.5. Likewise in throwing a die the probability of getting a deuce is 1:6 or 0.16, since there are six sides to a die. Conversely the odds against a head are even, or 1:1, or against throwing a deuce are 5:1. In statistical work, probability is the form generally used, and it is expressed as P = some decimal fraction.

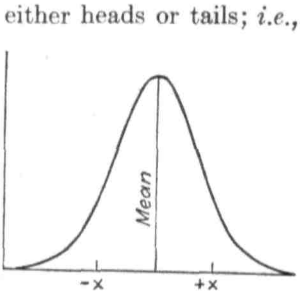

FIG. 119.—A normal curve.

If we erect an ordinate at point $+x$ in the normal curve (Fig. 119), we divide the area of the curve into unequal parts.

Since the area of the whole curve is proportional to the frequency of all the variates and the portion beyond $+x$ is proportional to all the variates beyond $+x$, it follows that the probability of selecting at random any variate beyond $+x$ is given by the ratio of the area beyond $+x$ to the whole area of the curve.

It has been proved that for all normal curves the ratio x/σ (x being any deviation from the mean and σ being the standard deviation) bears a definite relation to the proportion into which the normal curve is divided by an ordinate raised at any deviation from the mean. Thus, when the deviation $x = \sigma$, or $x/\sigma = 1$, the area beyond x is always 0.15866 of the whole curve; and, when $x/\sigma = 2.5$, the area beyond x is always 0.00621 of the whole curve; and the same values, of course, hold for similar locations of $-x$. Thus the probability of randomly picking values outside the range $M \pm x$ is equivalent to the proportionate areas beyond $+x$ and $-x$, which are cut off by erecting ordinates at $+x$ and $-x$. Since we are dealing with a symmetrical curve, the areas beyond $+x$ and $-x$ are equal, and the probability is just twice that for any deviation greater than x in one direction only.

Tables have been prepared that show for practically all values of x the proportionate areas cut off by erecting ordinates at any points $+x$ or $-x$ from the mean. These are called tables of *probability integrals.*

Fisher's modification of the longer tables is shown as Table 29.

TABLE 29.—TABLE OF x*

The deviation in the normal distribution in terms of the standard deviation

P†	0.01	0.02	0.03	0.04	0.05	0.06	0.07	0.08	0.09	0.10
0.00	2.575829	2.326348	2.170090	2.053749	1.959964	1.880794	1.811911	1.750686	1.695398	1.644854
0.10	1.598193	1.554774	1.514102	1.475791	1.439521	1.405072	1.372204	1.340755	1.310579	1.281552
0.20	1.253565	1.226528	1.200359	1.174987	1.150349	1.126391	1.103063	1.080319	1.058122	1.036433
0.30	1.015222	0.994458	0.974114	0.954165	0.934589	0.915365	0.896473	0.877896	0.859617	0.841621
0.40	0.823894	0.806421	0.789192	0.772193	0.755415	0.738847	0.722479	0.706303	0.690309	0.674490
0.50	0.658838	0.643345	0.628006	0.612813	0.597760	0.582841	0.568051	0.553385	0.538836	0.524401
0.60	0.510073	0.495850	0.481727	0.467699	0.453762	0.439913	0.426148	0.412463	0.398855	0.385320
0.70	0.371856	0.358459	0.345125	0.331853	0.318639	0.305481	0.292375	0.279319	0.266311	0.253347
0.80	0.240426	0.227545	0.214702	0.201893	0.189118	0.176374	0.163658	0.150969	0.138304	0.125661
0.90	0.113039	0.100434	0.087845	0.075270	0.062707	0.050154	0.037608	0.025069	0.012533	0

* Table 29 is reprinted from Table I of Fisher's *Statistical Methods for Research Workers*, Oliver & Boyd, Edinburgh, by kind permission of the author and publishers.

† The value of P for each entry is obtained by adding the column value to that of the now. For example, for $x = 1.200359$, $P = 0.23$.

Our problem involving heights of horses showed a mean of 64 in. and a standard deviation of 1.83 in. What would be our chance (probability) of picking at random from the Percheron-horse population one that would measure 67 in. or more, assuming that the height of Percherons simulated a normal curve and that our derived values (statistics) for the mean and standard deviation are true estimates of these values for the population?

$$M = 64 \text{ in.} \qquad \text{and} \qquad M + x = 67 \text{ in.} \qquad \therefore x = 3 \text{ in.}$$

$$\frac{x}{\sigma} = \frac{3}{1.83} = 1.639$$

Table 29 shows that the nearest recorded value of $x/\sigma = 1.644854$, for $P = 0.10$. This tells us that our chance of randomly picking a horse that will measure 67 in. or more or 61 in. or less is 10 per cent or 1:10, so that our chance of picking a horse that will measure 67 in. or more in height is one-half this amount, or 5 per cent or 1:20; and, conversely, the chance against being able to do so is 19:1. Similarly, we could estimate our chance of being able to pick outside of a range of $M \pm 2\sigma$, *i.e.*, horses that would measure less than 60.34 in. or more than 67.66 in. This deviation is 2σ or $x/\sigma = 2$. The nearest reading in the table is 1.959964 for $P = 0.05$. So the chance of randomly picking horses that will stand 67.66 in. and over is 1:40, or the chance against such selection is 39:1.

Standard Error.—Since a mean based on 1,000 randomly chosen observations would obviously be more trustworthy than one based on 10, and since a narrower curve would be more reliable than a wider one, for in the former a relatively smaller number of individuals will designate

the character of the population, the size and the variability of the sample studied can be used to measure the reliability of the results obtained from the sample. The standard deviation of a sample of n variates is σ, and the standard deviation of the mean of the sample is $\sigma/\sqrt{n}$. This is called the *standard error*, and it is in reality an estimate of the dispersion or standard deviation of a hypothetical population of means.

σ = standard deviation, applies to the individual variates

$\frac{\sigma}{\sqrt{n}}$ = standard error, applies to means of various samples of the whole population

Individuals picked at random from a population tend to simulate a normal curve. If a number of random selections were made and the means computed, these means would also tend to simulate a normal curve. Therefore, with means from samples, the table for the normal curve (Table 29) can be used to determine the probability that any mean will differ by more than any specified quantity from the true mean of the population.

In our example of horse heights, the mean or average height was 64 in., and the standard error is $\sigma/\sqrt{n}$ or $1.83/5.48 = 0.334$. Let us determine whether the true mean lies outside a range of ± 1 in., *i.e.*, between 63 and 65 in. Since we are concerned with the dispersion of means rather than variates, we must use for the value of x/σ in Table 29 the relation of x to the standard error, or $\frac{x}{\text{standard error}}$ or $\frac{1}{0.334} = 2.994$. The nearest reading in the table is 2.575829 for $P = 0.01$. The chance that the true mean lies outside the limits of 63 and 65 in. is less than 1:100.

The standard error of a mean is as we have seen

$$E_m = \frac{\sigma}{\sqrt{n}}$$

The standard error of the standard deviation is

$$E_\sigma = \frac{\sigma}{\sqrt{2n}}$$

The standard error of the coefficient of variation is

$$E_c = \frac{C}{\sqrt{2n}} \sqrt{1 + 2\left(\frac{C}{100}\right)^2}$$

and where C is less than 10 per cent the quantity under the second radical may be omitted.

The standard error of a statistic is placed directly after the statistic with a plus-minus sign ($\pm$) between the two. Thus, in our example

of the height of 30 Percheron horses ($M = 64$; $\sigma = 1.83$; $n = 30$), the mean would be written 64 ± 0.334; the standard deviation 1.83 ± 0.236; and the coefficient of variation 2.86 ± 0.369.

The usefulness of the standard error in measuring the reliability of a constant is dependent upon certain relations between the normal curve and its standard deviation. Normal curves may differ from each other considerably in variability, or, in other words, they may have very different standard deviations; but in one respect they are all alike, namely, in the proportion of their area (or the number of individuals which this represents) which is included between the mean and any multiple of the standard deviation. In Fig. 120 there is represented a typical normal curve, with perpendiculars erected below and above the mean at points once, twice, and three times the distance of the standard deviation from the mean. It can be proved that the area of the curve which is included between the perpendiculars at -1σ and $+1\sigma$ is .6826 of the whole; between -2σ and $+2\sigma$, .9544; and between -3σ and $+3\sigma$, .9975. Table 30 gives the percentages of the total area of the curve included between the limits set by various multiples of the standard deviation above and below the mean, and also the percentages of the curve lying outside these limits. Regardless of the absolute size of the standard

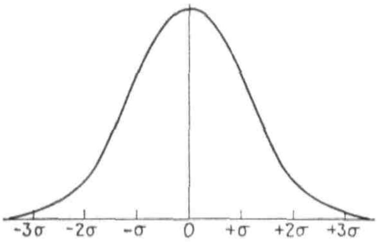

FIG. 120.—A typical normal curve.

TABLE 30.—PERCENTAGES OF THE NORMAL CURVE LYING BETWEEN, AND LYING OUTSIDE OF, THE LIMITS SET BY THE MEAN PLUS AND MINUS VARIOUS MULTIPLES OF THE STANDARD DEVIATION

Multiple of standard duration	Percentage of total area of normal curve lying between mean plus this multiple and mean minus the multiple	Percentage of total area of normal curve lying outside these limits
0.2	15.86	84.14
0.4	31.08	68.92
0.6	45.14	54.86
0.8	57.62	42.38
1.0	68.26	31.74
1.2	76.98	23.02
1.4	83.84	16.16
1.6	89.04	10.96
1.8	92.82	7.18
2.0	95.44	4.56
2.2	97.22	2.78
2.4	98.36	1.64
2.6	99.06	0.94
2.8	99.48	0.52
3.0	99.74	0.26

deviation (and thus of the variability of the curve), these values are the same for all normal curves and thus theoretically for all populations which vary solely by chance for any quantitative trait.

The importance of this property of the normal curve for our present problem is now obvious; for if the value of the standard error of a constant is known (which is simply the standard deviation of a population of constants similarly derived), we shall have a criterion of the reliability of this constant. Since 68.26 per cent of a normal curve (and thus of a population distributed purely by chance) may be expected to fall within the limits set by the mean plus its standard deviation and minus its standard deviation, we know the limits within which a constant derived from another sample may be expected to fall 68.26 per cent (approximately two-thirds) of the time.[1]

Thus the figure for the mean height of our Percheron horses,

$$64 \pm 0.334,$$

tells us that another sample from the same population would have, about two times out of three, a mean between $64 + 0.334$, or 64.334 in., and $64 - 0.334$, or 63.666 in. The standard error for the other constants is to be interpreted in the same way. It is evident that the size of the standard error measures the reliability of any statistic. A mean of 64 ± 14.0 for our horses would indicate that another sample would in two out of three cases have a mean somewhere between 50 and 78 in. The latitude here is so great as to make the statistic relatively valueless since another sample from such a population, while it would in two cases out of three fall between 50 and 78 in., has a good chance of being rather far removed from the determined mean of 64 in.

Probable Error.—The probable error, which was formerly used in biometrical work, is simply 0.6745 times the standard error in a normal curve or the quartile. This measures the limits within which one-half the area of the normal curve is included and thus within which the chance is *even* that a statistic derived from another sample will fall. This statistic has largely been superseded by the standard error in biometrical work.

Statistical Significance.—Many experiments are conducted as comparisons between two more or less similar variables; *e.g.*, a comparison between rations *A* and *B*; a comparison between two inbred lines of animals; comparisons between breeds, etc. We might, for instance, now go and measure 30 Thoroughbred horses. If these showed a different mean height from the Percherons, we would like to know whether this difference is due to unavoidable variations between the two samplings, generally termed *errors of random sampling*, or due to fundamental

[1] SINNOTT, EDMUND W., and DUNN, L. C., "Principles of Genetics," 3d ed., pp. 148–149, McGraw-Hill Book Company, Inc., New York, 1939.

TABLE 31.—TABLE OF t*

n	P = 0.9	0.8	0.7	0.6	0.5	0.4	0.3	0.2	0.1	0.05	0.02	0.01
1	0.158	0.325	0.510	0.727	1.000	1.376	1.963	3.078	6.314	12.706	31.821	63.657
2	0.142	0.289	0.445	0.617	0.816	1.061	1.386	1.886	2.920	4.303	6.965	9.925
3	0.137	0.277	0.424	0.584	0.765	0.978	1.250	1.638	2.353	3.182	4.541	5.841
4	0.134	0.271	0.414	0.569	0.741	0.941	1.190	1.533	2.132	2.776	3.747	4.604
5	0.132	0.267	0.408	0.559	0.727	0.920	1.156	1.476	2.015	2.571	3.365	4.032
6	0.131	0.265	0.404	0.553	0.718	0.906	1.134	1.440	1.943	2.447	3.143	3.707
7	0.130	0.263	0.402	0.549	0.711	0.896	1.119	1.415	1.895	2.365	2.998	3.499
8	0.130	0.262	0.399	0.546	0.706	0.889	1.108	1.397	1.860	2.306	2.896	3.355
9	0.129	0.261	0.398	0.543	0.703	0.883	1.100	1.383	1.833	2.262	2.821	3.250
10	0.129	0.260	0.397	0.542	0.700	0.879	1.093	1.372	1.812	2.228	2.764	3.169
11	0.129	0.260	0.396	0.540	0.697	0.876	1.088	1.363	1.796	2.201	2.718	3.106
12	0.128	0.259	0.395	0.539	0.695	0.873	1.083	1.356	1.782	2.179	2.681	3.055
13	0.128	0.259	0.394	0.538	0.694	0.870	1.079	1.350	1.771	2.160	2.650	3.012
14	0.128	0.258	0.393	0.537	0.692	0.868	1.076	1.345	1.761	2.145	2.624	2.977
15	0.128	0.258	0.393	0.536	0.691	0.866	1.074	1.341	1.753	2.131	2.602	2.947
16	0.128	0.258	0.392	0.535	0.690	0.865	1.071	1.337	1.746	2.120	2.583	2.921
17	0.128	0.257	0.392	0.534	0.689	0.863	1.069	1.333	1.740	2.110	2.567	2.898
18	0.127	0.257	0.392	0.534	0.688	0.862	1.067	1.330	1.734	2.101	2.552	2.878
19	0.127	0.257	0.391	0.533	0.688	0.861	1.066	1.328	1.729	2.093	2.539	2.861
20	0.127	0.257	0.391	0.533	0.687	0.860	1.064	1.325	1.725	2.086	2.528	2.845
21	0.127	0.257	0.391	0.532	0.686	0.859	1.063	1.323	1.721	2.080	2.518	2.831
22	0.127	0.256	0.390	0.532	0.686	0.858	1.061	1.321	1.717	2.074	2.508	2.819
23	0.127	0.256	0.390	0.532	0.685	0.858	1.060	1.319	1.714	2.069	2.500	2.807
24	0.127	0.256	0.390	0.531	0.685	0.857	1.059	1.318	1.711	2.064	2.492	2.797
25	0.127	0.256	0.390	0.531	0.684	0.856	1.058	1.316	1.708	2.060	2.485	2.787
26	0.127	0.256	0.390	0.531	0.684	0.856	1.058	1.315	1.706	2.056	2.479	2.779
27	0.127	0.256	0.389	0.531	0.684	0.855	1.057	1.314	1.703	2.052	2.473	2.771
28	0.127	0.256	0.389	0.530	0.683	0.855	1.056	1.313	1.701	2.048	2.467	2.763
29	0.127	0.256	0.389	0.530	0.683	0.854	1.055	1.311	1.699	2.045	2.462	2.756
30	0.127	0.256	0.389	0.530	0.683	0.854	1.055	1.310	1.697	2.042	2.457	2.750
∞	0.12566	0.25335	0.38532	0.52440	0.67449	0.84162	1.03643	1.28155	1.64485	1.95996	2.32634	2.57582

* Table 31 is reprinted from Table VI of Fisher's *Statistical Methods for Research Workers*, Oliver & Boyd, Edinburgh, by kind permission of the author and publishers.

So our formulas for studying and interpreting variation are:
By long method,

$$\text{Mean} = \text{arithmetical average} = \frac{\Sigma \text{ all variates}}{n}$$

$$\text{S.S.} = \Sigma(y - M)^2$$

$$\sigma = \sqrt{\frac{\Sigma(y - M)^2}{n - 1}} \text{ or } \sqrt{\frac{\text{S.S.}}{n - 1}}$$

$$\text{Variance} = \frac{\text{S.S.}}{n - 1} = \sigma^2$$

By short method (M_a = assumed mean),

$$M = M_a + \frac{\Sigma(y - M_a)}{n}$$

$$\text{C.F.} = \frac{[\Sigma f \cdot (y - M_a)]^2}{n}$$

$$\sigma = \sqrt{\frac{\Sigma f \cdot (y - M_a)^2 - \text{C.F.}}{n - 1}}$$

$$E_m = \frac{\sigma}{\sqrt{n}}$$

$$E_\sigma = \frac{\sigma}{\sqrt{2n}}$$

$$E_D = \sqrt{E_A^2 + E_B^2}$$

Significance = D greater than twice its standard error
Significance = D/E_D greater than x(2+ for large numbers, use table of x)
Significance = $\frac{D}{E_D}$ greater than t for $P = 0.05$ and n the degrees of freedom, use table of t

Coefficient of Correlation.—Correlation is a measure of the degree of association between two or more factors. Since pulling power in horses would seem to be at least in part due to weight, we would expect to find an association between heavy horses and pulling power, and we would expect this to be a positive association (correlation); *i.e.*, the heavier horses on the average would be more powerful than lighter horses. Since the production of milk involves the conversion of feed energy into milk and since there is more energy in fat than in carbohydrate or protein, we would expect that the milk produced by cows yielding 30,000 lb. a year would have a lower butterfat test than those producing 8,000 lb. a year—in other words, a negative association or correlation. Since it does not

seem logical to think that the color of the hair of a beef animal or hog would have very much association with the respective animal's ability to make rapid gains in weight, we would expect no correlation between coat color and ability to fatten.

TABLE 32.—HEIGHT OF MARES AND DAUGHTERS

Mare	Height x	Deviation from mean height of dams d_x		Square of deviation d_x^2	Daughter's height y	Deviation from mean height of daughters d_y		Square of deviation d_y^2	Product deviation $d_x \cdot d_y$	
		+	−			+	−		+	−
1	63	. .	1	1	60	. .	3	9	3	
2	64	0	. .	0	60	. .	3	9	0	
3	66	2	. .	4	65	2	. .	4	4	
4	65	1	. .	1	66	3	. .	9	3	
5	63	. .	1	1	58	. .	5	25	5	
6	62	. .	2	4	61	. .	2	4	4	
7	60	. .	4	16	62	. .	1	1	4	
8	64	0	. .	0	64	1	. .	1	0	
9	65	1	. .	1	66	3	. .	9	3	
10	66	2	. .	4	61	. .	2	4	. .	4
11	63	. .	1	1	61	. .	2	4	2	
12	67	3	. .	9	65	2	. .	4	6	
13	64	0	. .	0	63	0	. .	0	0	
14	63	. .	1	1	64	1	. .	1	. .	1
15	62	. .	2	4	62	. .	1	1	2	
16	64	0	. .	0	64	1	. .	1	0	
17	67	3	. .	9	66	3	. .	9	9	
18	61	. .	3	9	58	. .	5	25	15	
19	64	0	. .	0	62	. .	1	1	0	
20	61	. .	3	9	62	. .	1	1	3	
21	63	. .	1	1	62	. .	1	1	1	
22	64	0	. .	0	63	0	. .	0	0	
23	65	1	. .	1	64	1	. .	1	1	
24	68	4	. .	16	67	4	. .	16	16	
25	64	0	. .	0	63	0	. .	0	0	
26	63	. .	1	1	63	0	. .	0	0	
27	65	1	. .	1	64	1	. .	1	1	
28	64	0	. .	0	63	0	. .	0	0	
29	66	2	. .	4	67	4	. .	16	8	
30	64	0	. .	0	64	1	. .	1	0	
	1,920 $M = 64$	20	20	98	1,890 $M = 63$	27	27	158	90	5
									85	

Correlation coefficient $(r) = \dfrac{85}{\sqrt{98 \times 158}} = +0.68.$

Correlation coefficients, therefore, may be positive if there is a positive association between the variables, negative if there is a negative association, or insignificantly small if there is no association between them. If positive deviations in one respect (x) coincide with positive deviations in another respect (y), we will have a positive correlation; and, if positive deviations in (x) coincide with negative deviations in another respect (y), we will have a negative correlation. A perfect positive correlation would be $+1$, a perfect negative correlation -1. In biological data the correlation coefficient ranges between these limits but never reaches them.

As an example of correlation we can use our original example of the 30 Percheron horses. Let's assume they are mares and each has a female offspring. Since it is logical to suppose that size or height is in part determined by genes and since these offspring get half their genes from their dams, we would expect to find an association between these mares and their daughters. We will suppose, too, that the nutrition, or feeding, and the general management of these mares and their daughters have been comparable, *i.e.*, not any better or worse for one group than for the other. If these assumptions are correct and we do find a sufficiently large positive association between the mares and their daughters, we will be justified in assigning the similarity to similarity of genes or to heredity.

In Table 32, the height of each mare's daughter has been recorded on the same line with the mare, so that there is a daughter-dam comparison in each horizontal line of the table. The last column of Table 32 was secured by multiplying the deviation for any x variate by the deviation of the corresponding y variate taking into consideration the plus or minus signs of each variate ($+x - x = -$; $+x + x$, or $-x - x = +$). The last column is called the *product-deviation column*, $d_x \cdot d_y$. The algebraic total of these product deviations is called the *sum of the products* or S.P., and with n pairs of readings the S.P. will have $n - 1$ degrees of freedom. Now the

$$\frac{\text{S.S.}}{\text{Number of degrees freedom}} = \text{variance or } (\sigma^2)$$

and

$$\frac{\text{S.P.}}{\text{Number of degrees freedom}} = \text{covariance}$$

therefore,

$$r(\text{correlation}) = \frac{\text{covariance } xy}{\sqrt{\text{variance } x \times \text{variance } y}}$$

and, since the readings are in pairs the number of degrees of freedom for each variance and the covariance are the same, therefore,

$$r = \frac{\text{S.P.}}{\sqrt{\text{S.S. } x \times \text{S.S. } y}}$$

It is seen that when positive deviations in x coincide with positive deviations in y, S.P. will have a high positive value and a high positive r will result, and similarly for negative with negative. If, however, positive deviations in x coincide with negative deviations in y, a high negative correlation will result. If there are about as many positive deviations in x coinciding with negative deviations in y, and positive y's with negative x's; in other words, the variation in the two factors is independent, there will result an insignificantly small correlation. If the covariance is minus, r will be minus, if positive, r will be positive.

Significance of a Correlation Coefficient.—Since chance might give a high value for r if n is small, the normal standard error for r, $1 - r^2/\sqrt{n}$ or $1 - r^2/\sqrt{n-1}$ is generally modified for the sake of greater accuracy or safety to $\sqrt{1 - r^2}/\sqrt{n-2}$.

The above formula used in conjunction with the table of t gives a critical test of the significance of a correlation coefficient, which has of necessity been devised from a limited number of pairs of observations. In our example, for instance, we have used only 30 pairs of mares and daughters, so we must be cautious about saying that there will always be found a high degree of association between dams and daughters as far as height is concerned.

$$t \text{ (by calculation)} = \frac{r}{\sqrt{1 - r^2}/\sqrt{n-2}}$$

$$= \frac{r \times \sqrt{n-2}}{\sqrt{1 - r^2}}$$

If we consult table of t and find that for $n - 2$ degrees of freedom the above indicated value of t corresponds to a value of P less than 0.05, we are justified in saying that the correlation coefficient is significant, *i.e.*, that there is an association between the two factors.

Substituting our derived figures (Table 32), in the formula, we have

$$t \text{ (by calculation)} = \frac{0.68 \times \sqrt{28}}{\sqrt{1 - 0.68^2}} = \frac{3.5972}{0.773} = 4.90$$

Consulting Table 31, for 28 degrees of freedom we find that the probability of exceeding this calculated value purely by chance is very much less than 0.01, because the reading for 0.01 is only 2.763. In other words the correlation of 0.68 between the heights of mares and their

daughters is highly significant, which is, of course, exactly what students of breeding would expect to be the case.

We could have done this problem by using the short method of guessing at the mean. We will set it up in that form and leave the solution to the student.

Height of mares, x	Height of daughters, y										f_x	d_x	$f \cdot d_x$	$f \cdot d_x^2$	$\Sigma d_x \cdot d_y$
	58	59	60	61	62	63	64	65	66	67					
60					1						1	−4			
61	1				1						2	−3			
62				1	1						2	−2			
63	1		1	1	1	1	1				6	−1			
64			1		1	4	3				9	0			
65							2		2		4	1			
66				1				1		1	3	2			
67								1	1		2	3			
68										1	1	4			
f_y	2	0	2	3	5	5	6	2	3	2					
d_y	−5	−4	−3	−2	−1	0	1	2	3	4					
$f \cdot d_y$															
$f \cdot d_y^2$															

FIG. 121.—A correlation table.

The student should practice with this and other problems until he becomes familiar with the technique of determining means, standard deviations, standard errors, and correlation coefficients and evaluating them in terms of their significance or lack of it.

As previously stated, correlation indicates the degree of association between variables. It does not, however, indicate that there is necessarily a causal relation between them. We might correlate the length of cows' teats with their milk production and assume that we secured a positive and significant correlation. This would mean that in the sample studied there was a high degree of association between long teats and high milk yield but it would not necessarily mean that the long teats caused the high production, or vice versa. On the other hand, it is reasonable to assume that positive correlations between rainfall and crop yields are due to the causal action of the water in promoting plant growth, or that the added pulling power of large horses is caused, in part at least, by their added weight. We must be accurate in gathering our data and in applying our formulas, but we must also be intelligent in interpreting the results secured.

When many variables are included or there are a number of intereacting factors, partial and multiple correlation techniques are applied in order to sift out the relative influence of each variable and its influence on the others. When there is an obvious relation between variables, the technique of the *regression function*, which "expresses the average value that may be expected from the variates in one factor for any given value of the correlated factor," is often of greater usefulness in studying interdependent relations than is the correlation coefficient.

Analysis of Variance.—For any group of statistical data, we may obtain the mean, standard deviation, coefficient of variation, and standard error, and by means of the table of x or table of t we may calculate the significance of these statistics. We may also employ the technique of correlation to ascertain the degree of association between two or more things.

Still another statistical technique is that of *analysis of variance.* The purpose of this technique, as the name implies, is to analyze the total variance into its component parts; *e.g.*, to separate that due to environmental causes from that due to heredity or that due to errors of random sampling within the sample from that due to differences between the means of each of two or more samplings. The process by means of which the total variance in a composite sample is accurately apportioned among the different factors or groups of causes responsible for its gross

TABLE 33.—HEIGHT OF HORSES IN SAME STUD 1930 AND 1940

Horse	1930 height	Deviation from mean 1930 height		Square of deviation	1940 height	Deviation from mean 1940 height		Square of deviation
	x	dx		dx^2	y	dy		dy^2
		+	−			+	−	
1	60	...	3.8	14.44	61	....	1.3	1.69
2	62	...	1.8	3.24	66	3.7	....	13.69
3	63	...	0.8	0.64	64	1.7	....	2.89
4	65	1.2	...	1.44	62	....	0.3	0.09
5	64	0.2	...	0.04	61	....	1.3	1.69
6	65	1.2	...	1.44	60	....	2.3	5.29
7	66	2.2	...	4.84	65	2.7	....	7.29
8	66	2.2	...	4.84	58	....	4.3	18.49
9	63	...	0.8	0.64	66	3.7	....	13.69
10	64	0.2	...	0.04	60	....	2.3	5.29
M	63.8	7.2	7.2	31.60	62.3	11.8	11.8	70.10
	S.S. 1930 = 31.60					S.S. 1940 = 70.10		
	Aggregate S.S. within series = 101.70.							

value is termed the *analysis of variance.* This not only allows the separation of the total variance into its several categories but also permits a single estimate of the standard deviation based on all the available data that can be used to measure the significance of the differences between the separate sets of data.

Where only two group means are being compared, either the t test or the F test will give an estimate of significance; where more than two group means are being compared the F test must be used.

Table 33 (page 438) shows the height of 10 horses taken in 1930 and another 10 horses in the same stud in 1940. We would like to know how much of the variance between these two groups of horses is due to errors of random sampling, how much of it is due to variation between the two groups, and whether or not the difference between the means of the 1930 and 1940 samples is significant.

TABLE 34.—TOTAL VARIANCE OF 1930 AND 1940 HORSES

Series	Height of horses	General mean	Deviation from mean		Square of deviations
			+	−	
1930 horses					
1	60	1,261/20 =	. . . . .	3.05	9.3025
2	62	63.05	. . . . .	1.05	1.1025
3	63		. . . . .	0.05	0.0025
4	65		1.95	. . . . .	3.8025
5	64		0.95	. . . . .	0.9025
6	65		1.95	. . . . .	3.8025
7	66		2.95	. . . . .	8.7025
8	66		2.95	. . . . .	8.7025
9	63			0.05	0.0025
10	64		0.95	. . . . .	0.9025
1940 horses					
1	61		. . . . .	2.05	4.2025
2	66		2.95	. . . . .	8.7025
3	64		0.95	. . . . .	0.9025
4	62		. . . . .	1.05	1.1025
5	61		. . . . .	2.05	4.2025
6	60		. . . . .	3.05	9.3025
7	65		1.95	. . . . .	3.8025
8	58		. . . . .	5.05	25.5025
9	66		2.95	. . . . .	8.7025
10	60		. . . . .	3.05	9.3025
			20.50	20.50	112.9500

This S.S. has 9 degrees of freedom from each series, or a total of 18. If the contributory sources to the total dispersion are all independent,

the S.S. from the complete data will be equal to the aggregate of the S.S. from each of these contributory sources, or 101.70.

We have put these data together in Table 34 (page 439) to get the general mean and the dispersion from the general mean (S.S.).

The variation between the series of the "1930 horses" and the "1940 horses" depends on the dispersion shown by the means of each series relative to the general mean of both series combined. This gives us the following:

Series	Mean of series	Mean of both series	Deviation from general mean		Square of deviation
			+	−	
1930 group	63.80		0.75	....	0.5625
1940 group	62.30	63.05	....	0.75	0.5625
					1.1250

The deviations in this calculation are means of 10 variates rather than of single variates, so in order to get a value representing the aggregate dispersion of the 10 variates in each sample, we must multiply the square of the deviations as calculated from the means by 10. The S.S. between series is, therefore, 1.1250 × 10 = 11.250. Since only two deviations were used in its determination, this S.S. has $n - 1$ or 1 degree of freedom.

Now we can analyze the variance as shown in Table 35.

TABLE 35.—ANALYSIS OF VARIANCE

Factor	S.S.*	Degree of freedom	Variance, or mean square S.S. ÷ degrees of freedom
Total	112.95	19	
Between series	11.25	1	11.25
Within series; *i.e.*, error	101.70	18	5.65

* It will be noticed that the total S.S. is the sum of the between-series and the within-series S.S., which means that the finding of any two of these three items permits finding the third by a simple arithmetical computation.

The within-series variance is a measure of the unavoidable variation between similar units (1930 or 1940 group) in the material from which the data have been collected, and the square root of this value is the best estimate of the standard deviation. Since the standard error of the means of series are calculated from the standard deviation, the within-series variance is generally called the *error variance*, or in this case $\sigma^2 = 5.65$ (and $\sigma = \sqrt{5.65}$).

$$\text{Standard error of the mean of the 1930 or 1940 group} = \sqrt{\frac{5.65}{10}}$$

Standard error of the difference between the means of the 1930 and 1940

$$\text{groups} = \sqrt{\frac{5.65 \times 2}{10}} = 1.063$$

In order to be significant the difference between the means must be greater than $t \times 1.063$, where t is the reading from the table of t (Table 31) for $P = 0.05$ and $n = 18$, which corresponds to the number of degrees of freedom in this case. This value is $2.101 \times 1.063 = 2.233$. Since the difference between the means of the ten 1930 horses and the ten 1940 horses is only 1.5 in., this is not a significant difference.

Since the t test cannot be used with more than two group means and also since the significance of many biological and agricultural data are reported in terms of the F test, it is expedient for the student of animal breeding to understand the main outlines of the latter test.

The mean squares, 11.25 and 5.65, are both independent estimates of the variance of an infinitely large and hypothetical population of horse heights. And on this basis they should be somewhat similar. Some discrepancy between the sizes of these two estimates of variance may be allowed because of chance fluctuations, but, if the difference is too great, we may suspect that the mean squares 11.25 and 5.65 are estimating the variances of different populations.

How great a difference between estimates of variance must be to be significant of a true difference is discovered by entering on the F table (see Snedecor)[1] with the appropriate degrees of freedom (in our case 1 and 18) and comparing the F in the table with the F obtained by dividing the larger mean square by the smaller, in our case $11.25/5.65 = 1.99$. If this F value is larger than the appropriate value listed in the table of F, we may have considerable confidence in the fact that there is a true difference between the heights of the 1930 horses and the heights of the 1940 horses.

The table of F in Snedecor shows values of 4.41 (significant) and 8.28 (highly significant) for 1 and 18 degrees of freedom. Because our value is only 1.99, we conclude that there is no significant difference between the height of horses in this stud in 1930 and 1940.

The above discussion pertains to the simplest type of analysis of variance. We will refer the student to textbooks of statistical techniques for more complex treatment of analyses of variance.

Summary.—The purpose of this chapter was to make the student a bit more wary of hastily drawn conclusions concerning biological differ-

[1] Snedecor, G. W., "Statistical Methods," pp. 184–188, Collegiate Press, Inc., of Iowa State College, Ames, Iowa, 1940.

ences by reminding him that such differences as our breeding animals exhibit may be due to heredity or to environment or both and to introduce him to some of the simpler devices for measuring and evaluating such differences as are found. There are many excellent texts available for those who wish to pursue the subject beyond this point.

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CHAPTER XIX

SEX DETERMINATION

Sex in the higher animals is a relative matter in all except one respect, *viz.*, the kinds of cells produced. And even in this respect the different types of cells, ova and spermatozoa, are essentially alike regarding chromosome content and differ only regarding cytoplasm and motility. For obvious reasons, man has always been keenly interested in the factors determining sex, with the hope that he might ultimately find ways and means of controlling them to his own benefit. Because of the wide interest and enormous value of such knowledge, there have been conceived in men's minds a great number of hypotheses regarding sex determination and its control. It is said that over 500 of these theories have been recorded. One theory states that the right testicle produces male-producing spermatozoa and the left testicle female-producing spermatozoa. The same idea is often applied to the ovaries of the female. Many breeders believe that alternate heat periods are productive of opposite sexes. The same idea is sometimes applied to service at early and late portions of the heat period. Such theories as these have easily been proved false. One of the most weird superstitions states that "if a man has a sty on his eye, he concludes his aunt is pregnant. If the sty is on the upper eyelid the offspring will be a boy; on the lower a girl." Any theory for sex determination must, from the very nature of the case, be correct half the time, the offspring, of necessity, being either male or female, in most species these occurring in equal numbers.

Sex Ratios.—In most of the higher species the two sexes are born in approximately equal numbers, whereas in some of the lower species there are great differences in numbers of the two sexes. Since in some of the multiparous species many embryos die and are absorbed during gestation, the actual number born is neither a correct record of fecundity nor is the sex ratio at birth necessarily the same as at fertilization if there is a differential survival rate between the sexes. Both Hammond and Parkes have shown that in swine there is a preponderance of males soon after fertilization, but in this species the males are more liable to die during embryonic development, so that at time of birth they exist in approximately equal numbers, and Parkes has reported the same phenomenon in mice. Other evidence indicates that in mammals,

generally, there is a heavier fetal death toll on the male than on the female embryos. For these reasons the sex ratio at fertilization is sometimes referred to as the *primary* sex ratio, that at birth as the *secondary*. In this discussion, sex ratio means that existing at birth.

Sex ratios are expressed as the number of males per 100 females or as the percentage of males of the whole number born. For statistical reasons the latter figure is preferred.

Table 36 gives some sex ratios that have been found in some of the higher animals.

TABLE 36.—SEX RATIOS IN FARM MAMMALS AND MAN*

Animal	Number of births studied	Percentage of males in all births	Number of studies
Horse	1,249,337	48.9–49.9	6
Mule	1,416	44.3	1
Cattle	155,579	49.4–51.5	3
Sheep	91,640	49.5	1
Swine	74,639	50.6–52.3	3
Goat	3,000	50.1	1
Man	....	50.7–51.7	Several

* Adapted from LUSH, J. L., "Animal Breeding Plans," p. 315, Collegiate Press, Inc., of Iowa State College, Ames, Iowa. 1937. (By permission of author and publisher.)

If sex is determined by the chromosomes and genes, as seems most probable, and the heterogametic spermatozoa (in mammals) are produced in approximately equal numbers, then differences in fertilization rate must be due to differential activity of the two types of spermatozoa or to differential selectivity by the ova. If there is a differential fertilizing rate between the male- and female-conditioning sperm but approximately equal numbers of the sexes at birth, then there must also be a differential mortality rate between the two types of embryos, with the male embryo in mammals apparently having a higher rate of mortality.

Chromosomes and Sex Determination.—*Drosophila melanogaster*, the common fruit fly, has been more thoroughly studied, from the standpoint of inheritance, than any other species, and the study has yielded a rich harvest. Along with the knowledge gained regarding behavior of genes and chromosomes in transmission from parent to offspring has come definite knowledge regarding sex and what determines it. There are two sources of such information, one cytological and the other the behavior of sex-linked factors. Cytology has established the fact that the normal number of pairs of chromosomes in *D. melanogaster* is four. Of these, three pairs are autosomes and one pair sex chromosomes, and although both sexes have autosomes that are morphologically identical, there is a characteristic difference between male and female

regarding the sex chromosomes. The female has two so-called X chromosomes, whereas the male has one X chromosome and one Y chromosome. Figure 122 should make this clear.

After reduction has taken place, as shown in the diagram, there can be but one sort of ovum produced; *i.e.*, every ovum will contain one member of each pair of chromosomes, and each one will, therefore, contain one X chromosome. In the male, after reduction, there will be two kinds of spermatozoa, both of which are similar as to autosomes but different as to sex chromosomes, one having an X chromosome and the other a Y chromosome. Presumably, these kinds of spermatozoa are produced in equal numbers. Starting with an ovum containing an X chromosome and adding a spermatozoon also containing an X chromosome will give an individual with two X chromosomes, or a female.

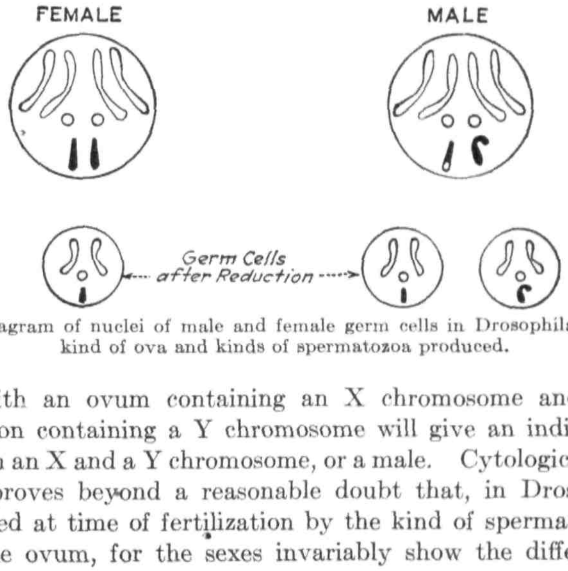

FIG. 122.—Diagram of nuclei of male and female germ cells in Drosophila, showing the kind of ova and kinds of spermatozoa produced.

Starting with an ovum containing an X chromosome and adding a spermatozoon containing a Y chromosome will give an individual containing both an X and a Y chromosome, or a male. Cytological evidence, therefore, proves beyond a reasonable doubt that, in Drosophila, sex is determined at time of fertilization by the kind of spermatozoon that fertilizes the ovum, for the sexes invariably show the differences just outlined.

Nondisjunction in Drosophila.—An aberrant type of reduction in Drosophila, occurring very rarely, lends support to the chromosomal interpretation of sex determination. This is the feature of nondisjunction, which has been worked out by Bridges. This investigator has shown that occasionally reduction in the germ cells takes place in such a way that after synapsis the two sex chromosomes of a female do not disjoin but both of them pass to one pole of the cell, giving rise to egg cells of the constitution XX and O instead of two normal egg cells, each containing one X chromosome. The relations holding may be made more clear by means of introducing a sex-linked character. If,

for instance, a white-eyed female ($rXrX$) is mated to a red-eyed male (RXY), all the normal daughters will be red-eyed and the normal males white-eyed.

Sperms	Eggs	
	rX	rX
RX	$RX\ rX$	$RX\ rX$
Y	rX Y	rX Y

If, however, in a white-eyed female, nondisjunction occurs, individuals of the four types indicated in the diagram below should be produced.

Sperms	Eggs	
	$rX\ rX$	O
RX	$RX\ rX\ rX$	RX O
Y	$rX\ rX$ Y	Y O

As a matter of fact, the $RXrXrX$ individuals usually die, as do also the YO individuals, the former, as Morgan suggests, because of too many X's and the latter presumably because they lack an X chromosome. In other words, if the genetic constitution is thrown too far out of balance, the animal cannot survive. The other two individuals $rXrXY$, a white-eyed daughter, and RXO, a red-eyed male, are the exceptions to the normal expectancy.

Breeding results from such individuals in F_2 (which the student can diagram) give results that would be expected from individuals of such chromosomal make-up, and the point to be stressed here is that, in either F_1 or F_2 individuals, two X chromosomes result in producing a female and one X chromosome a male.

These results not only furnish very strong proof of the chromosome theory of sex, but serve also to show how a knowledge of the actual mechanism involved leads to the discovery of how a change in the mechanism gives a new output. The conclusion that females behaving in this manner must contain a Y chromosome was confirmed by the cytological demonstration that showed in them two X's and a Y.[1]

The distinguishing feature of the XY type of sex inheritance, which prevails in mammals, is that the female is homogametic and the male heterogametic for the sex chromosome. It was thought at one time

[1] MORGAN, T. H., "The Physical Basis of Heredity," p. 203, J. B. Lippincott Company, Philadelphia, 1919.

that the Y chromosome was simply a neutral and more or less useless mate for the X chromosome. This, however, has been disproved. Only one dominant gene has been demonstrated in the Y chromosome of Drosophila, but the fact that all males of the genetic constitution XO, *i.e.*, lacking a Y chromosome, are sterile leads one to the conclusion that something in the Y chromosome is essential for fertility—in other words, for normal maleness. It is known that in some species certain characteristics are passed along always and only from father to son, indicating that their determiners must be in the Y chromosome.

The Theory of Genic Balance.—In several species of animals, there have been found individuals that partook partly of the characteristics of both sexes, *i.e.*, were in fact partly male and partly female. This was difficult to explain on the basis cited above: that one X results in producing a male and two X's a female. Goldschmidt first studied these so-called "intersexes" in the gypsy moth *Lymantria dispar*. He found that in the F_2 of a cross between Japanese males and European females half the daughters were intersexes. Goldschmidt after an extended genetic study concluded that sex was due to a balance between male- and female-producing genes in the sex chromosomes.

These and other crosses leave no doubt that the tendency to form intersexes is inherited in a regular manner. In moths, in general, the males are XX, the females XY; and within pure races this sex chromosome constitution is decisive. In crosses between races which produce intersexes, however, two further variables have to be taken into account; one is a factor for maleness in the sex chromosome which has different strengths, that is, presumably occurs in different allelic forms in different races; the other is an influence tending in the opposite direction toward femaleness; also varying in different races, and this seems to be inherited through the cytoplasm of the eggs, that is, all the eggs of an individual are alike with respect to the strength of this tendency. The sexual condition of the offspring of crosses is decided by the relative strengths or balance existing between these two opposed tendencies. This interpretation is supported by extensive evidence from many interracial crosses.

Goldschmidt and his coworkers have also proposed a mechanism by which these sex genes influence the development of the sexual characters. The essential assumptions here, as found first in the worm Bonellia, established by a careful study of the embryological development of Lymantria and later extended to Drosophila, are that intersexes in these forms begin their development as males (or females) and develop as such up to a certain critical point, the so-called "turning point," after which their development is of the opposite sexual type. The mixture of male and female parts is thus explained as due to the supersession of one type of sex tendency by the other. Sex development is conceived as essentially a competition between opposed tendencies in which the race is eventually won by that type of process (either male or female) which proceeds most rapidly at the critical period of determination of each organ or part involved.[1]

[1] SINNOTT, EDMUND W., and DUNN, L. C., "Principles of Genetics," p. 261, McGraw-Hill Book Company, Inc., New York, 1939.

The discovery of certain individuals in Drosophila cultures, which in their sex characteristics were between (intersexes) or beyond (supersexes) the normal male or female limits, has yielded further evidence that sex manifestations are due to a certain balance between the genetic content of the automosomes and that of the sex chromosomes. Bridges has shown that the normal balance between two sets of autosomes (2*A*) and two sex chromosomes (2X) produces a female, and the balance between 2*A* and 1X produces a male. That is to say, the autosomes have genes tending to produce maleness, which they do when working in conjunction with the genes found in one X chromosome. When, however, there are 2X chromosomes present working in conjunction with 2*A*, the result is a female; *i.e.*, the genes in the X chromosomes are preponderately female-producing. A graded series of sexes have been found or produced experimentally as indicated in Table 37.

It will be seen from this table that a normal balance between autosomes and sex chromosomes 3*A* and 3X or 2*A* and 2X results in a female, whereas a preponderance of the X ingredient results in a superfemale and a preponderance of the autosomal ingredient results in varying degrees of manifestations of maleness.

If we represent the net effectiveness of the female tendency genes in the X by 100, then we should represent the net male effectiveness of a set of autosomes by some lower number, approximately 80. In the 2X2*A* individual the ratio of female effectiveness to male effectiveness is 200:160, or 1.25:1. On this formulation an index of 1.25 corresponds to a normal female. As is indicated in Table 37, this same index of 1.25 holds for 3*N* individuals, for the ratio is 300:240, or 1.25:1. The identity of sex indices for the 3*N* and 2*N* forms corresponds to the observation that there seems to be no sexual difference between them. In the X2*A* individual the ratio is 100:160, or the sex-index is 0.63, that of the standard male. The sex-index of the 2X3*A* intersex is 0.83, intermediate between the 1.25 of femaleness and the 0.63 of maleness.

TABLE 37.—RELATION OF SEX TO CHROMOSOMES IN *Drosophila melanogaster*

Sex type	Formula	X = 100	*A* = 80	Sex index
Superfemale	2*N* . . . 3X:2*A*	300	160	1.88
	4*N* . . . 4X:4*A*	400	320	1.25
Female	3*N* . . . 3X:3*A*	300	240	1.25
	2*N* . . . 2X:2*A*	200	160	1.25
	1*N* . . . 1X:1*A*	100	80	1.25
Intersex	4*N* . . . 3X:4*A*	300	320	0.94
	3*N* . . . 2X:3*A*	200	240	0.83
Male	2*N* . . . 1X:2*A*	100	160	0.63
	4*N* . . . 2X:4*A*	200	320	0.63
Supermale	3*N* . . . 1X:3*A*	100	240	0.42

New tests of the general validity of the genic balance formulations as a ratio between opposed sets of genes came from several sources. First, both myself [Bridges, 1925] and L. V. Morgan found tetraploid individuals. We observed that these 4X4A individuals were completely normal and fertile females, practically indistinguishable somatically from $3N$ females. That the sex was not changed when the chromosomes were doubled is in the best conformity with the ratio formulation and is difficult to account for on the arithmetical system (Schrader and Sturtevant 1923).

A second and more striking test came from the work with the haploid or one N individual in Drosophila. It was predicted that this type should be female in sex since it must have the same ratio of X to A as the $2N$, $3N$, and $4N$ females.

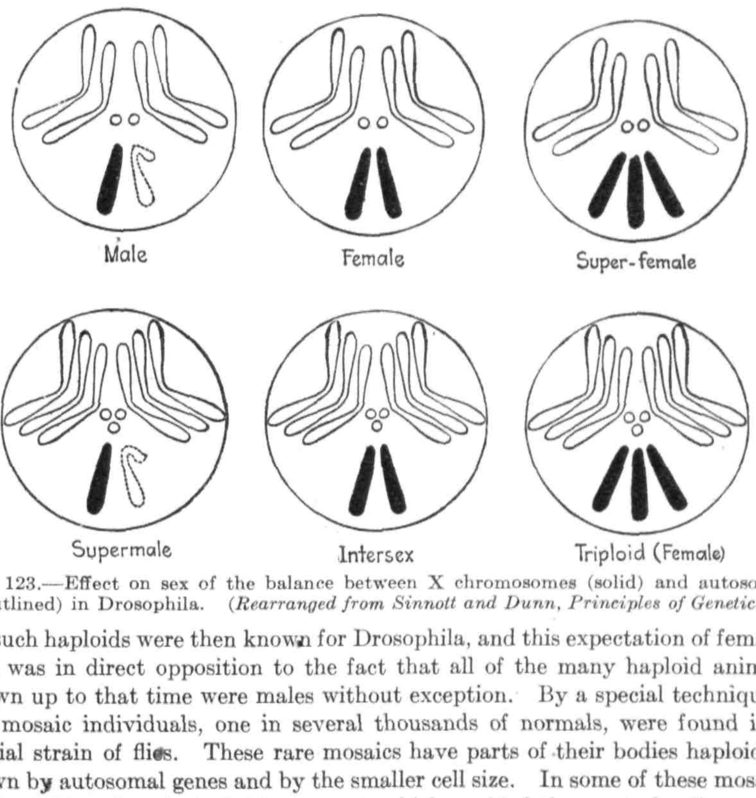

FIG. 123.—Effect on sex of the balance between X chromosomes (solid) and autosomes (outlined) in Drosophila. (*Rearranged from Sinnott and Dunn, Principles of Genetics.*)

No such haploids were then known for Drosophila, and this expectation of femaleness was in direct opposition to the fact that all of the many haploid animals known up to that time were males without exception. By a special technique a few mosaic individuals, one in several thousands of normals, were found in a special strain of flies. These rare mosaics have parts of their bodies haploid as shown by autosomal genes and by the smaller cell size. In some of these mosaics the haploid regions included body parts which enabled the sex to be diagnosed. They were actually female as expected (Bridges 1925). Since then at least three other workers have found Drosophila mosaics in which haploidy and femaleness seem to be associated.

In unpublished results Sturtevant has found that the 2X4A is a male and that 3X4A individuals are intersexes, both fitting into place in the series.

The observation of $1N$ = ♀ in Drosophila no longer stands alone. Frankhauser (1937) secured haploid embryos of the newt, one of which lived nearly

give rise to gynandromorphs. Definite proof of the occurrence of such dizygotic gynandromorphs came in Drosophila with the discovery of sex-mosaics which were at the same time mosaics for autosomal marker characters. Occasionally such dizygotics were mosaics for autosomal characters in two different autosomes, though it is rare to make a cross that would show this. The first of the clear dizygotic gynandromorphs was one found by Bridges (Morgan, Bridges, and Sturtevant, 1925) in a backcross involving two second-chromosome recessives, vestigial and speck. The right side of the body was mostly female and showed speck; the left side was mostly male and showed vestigial. The explanation is that the right side had come from an X-egg carrying speck, fertilized by an X-sperm carrying vestigial and speck. The left side came from an X-egg carrying vestigial, fertilized by a Y-sperm carrying vestigial and speck. Some 20 dizygotic mosaics have been found in Drosophila, though the majority were alike in sex on the two sides.

In Drosophila there is another type of gynandromorph, of which several hundred have been found. These start as XX zygotes and give rise to XO male tissues on one side or part of the body. The male tissue results from the loss or "elimination" of one of the two original X chromosomes, the autosomes all remaining diploid. If the elimination takes place at the first cleavage, half of the body becomes male; if at the second, only about a quarter.

A striking example of such a bilateral gynandromorph was one found by A. M. Brown and included in the general account of gynandromorphs by Morgan and Bridges (1919). This gynandromorph occurred in a cross between an eosin miniature male and a female heterozygous for eosin and miniature. The male right side showed miniature and eosin, while the left side was female and wild-type. Presumably the gynandromorph started from an eosin miniature/wild zygote and at the first cleavage division one of the daughter chromosomes of the maternal wild type X chromosome lagged upon the spindle and was lost. Hence one cell retained the original constitution and developed as female while the other was XO in constitution and developed as eosin miniature male.

In case the male parts of an elimination gynandromorph include the abdomen, such an individual can be mated as a male. But he is invariably sterile, as he should be from the XO constitution of the male parts.

That an X-chromosome only, and not the autosomes, is involved in the elimination was shown by a test proposed by Muller, namely that a cross be made involving the sex-linked characters yellow and white, as markers for the X, and ebony or some other recessive as a marker for the autosomes. Gynandromorphs in such crosses showed sex-linked characters in the male parts but never the autosomal ones—except those due to double fertilization, as noted above.

Morgan and Bridges (1919) studied carefully about 100 gynandromorphs and found that the maternal X was eliminated about as frequently as the paternal X. In experiments in which all flies were counted 40 gynandromorphs occurred in 88,000 flies, or 1 in 2200. The line of separation was usually sharp with respect to both sex and whatever sex-linked characters showed in the different areas. Of the dozens of sex-linked characters seen in the gynandromorphs all were autonomous in development locally except vermilion, and, to a slight extent Bar (Sturtevant 1920).

A third type of sex-mosaic was found by Bridges (1925) in crosses in which the mother was heterozygous for the sex-linked dominant Minute-*n* and the father showed one or more sex-linked recessives, such as yellow, eosin and singed. The Minute-*n* daughters frequently (10 to 40 per cent) showed one or more spots that were not Minute, but were yellow eosin and singed. Some of these spots could be classified as male by including eosin (lighter in ♂) or the fore-leg with its sex comb. The explanation offered by Bridges was that Minute-*n* induced frequent elimination of the *Mn*-bearing X in the somatic calls. This occurred relatively late in imaginal disc development, thus accounting for the small size of the spots. But Stern (1936) has studied their origin thoroughly and shows that they are due to crossing-over in the imaginal cells. This crossing-over leads automatically to somatic segregation, since the equational separation of spindle-attachments draws the crossover terminal regions into separate cells. Stern finds that the homozygous *Mn* spots then die, leaving the homozygous *y sn* spots which were observed by Bridges. Stern finds that most spots are XX and female. Male spots, such as those detected by Bridges, do occur, principally when the *Mn* mother carries an extra Y chromosome. Then somatic segregation gives XY male spots, instead of XO spots as Bridges supposed.[1]

Endocrine Function in Sex Differentiation.—In the earliest forms of life, there probably were no distinct sexes. These organisms reproduced only by fission, or budding, where the division of the parent was very unequal. This, of necessity, meant that the offspring would be very similar to their parents, for a considerable portion of the parent went to form each new offspring, although an occasional mutation might happen. Eventually the division of labor among the cells making up organisms meant that certain cells were developed for the particular purpose of reproduction. At length, there apparently came to be formed different types of reproductive cells, which had to unite to produce a new organism. At first these cells were produced by one parent (hermaphrodite), but eventually there came a time when the union of dissimilar cells, particularly as far as cytoplasm is concerned, produced by two separate individuals was necessary to form the beginning of a new individual, and finally the two sexes themselves came to be quite different, in part because of the constitution that allowed one to produce eggs and the other spermatozoa. Sexuality has therefore come about through a long line of evolutionary development, and the advent of unisexuality probably greatly speeded up the evolutionary process because of the gene differences brought together in the new organism, and the fact that the new organism in turn was destined to give a random, sample half of its diversely acquired genetic material to each of its offspring.

Many plants and animals are still of one sex in one portion of the body and the other sex in another portion. In some the production of male or female gametes alternates or varies in time owing probably to environ-

[1] *Ibid.*, pp. 25–28.

mental influences. In higher mammals, of course, the two sexes are recognizably different both in regard to their sexual products (eggs and spermatozoa) and their somatic differentiation. These differences are basically genetic, *i.e.*, owing to differences in gene complements, but superimposed on the genic differences are those lately discovered to be of an endocrine nature.

It is probable that in Drosophila and many other species of lower animals the same mechanism, *i.e.*, the genes, underlies both these phenomena. If, at the first cell division in a female Drosophila zygote, one of the resulting daughter cells gets only one X chromosome, a gynandromorph half male and half female results. If the discrepancy occurs at the second cell division, approximately one-quarter of the resulting organism will show male characteristics.

In the higher vertebrates, however, the evidence indicates that, although the genic balance usually determines the sex of the individual, this is subject to another, hormonal, control. Lillie has shown that the freemartin (abnormal sexual female) in cattle arises where the choria of unlike sexed twins become fused and the blood vessels anastomosed so that the blood of the two embryos becomes interchangeable. Lillie has shown that this is due to the influence of a hormone secreted by the male gonad which, when carried by the blood into the female calf, replaces the development of normal ovaries and, to some extent, the female accessory organs of reproduction with testes and male ducts. The female is genetically a female and appears phenotypically as a female, but the male sex hormone in its blood during early embryonic life prevents the development of a normal set of female genital organs and substitutes an imperfect male set. Hughes has reported the same phenomenon in the pig. Specifically, the medullary portion of the gonad forms sex cords instead of the normal medullary cords of an ovary.

Experimentally, this has been accomplished in several of the lower animals by surgically joining embryos, by gonad transplantations, and by the injection of sex hormones into embryos. The female sex hormone injected into an embryonic genetic male chick causes the left testis to become a flattened, ovarylike, ovotestis, and the right testis is sometimes affected and the oviducts persistent. Injection of the male sex hormone into an embryonic, genetic female causes the cortex of the left ovary to thin out and the medulla to hypertrophy and transform into testicular tissue at the hilus.

The first set of sex cords that pass into the gonad form the medulla, and this later forms the sex cords of the male. The medulla is present in the ovary, and later there is added the cortex. The ovary, therefore, consists of two tissues of different physiological capacities. In the early

stages, the male gonad also has a cortex, but this does not persist. The seminal cords of the medulla are already established at the time of morphological sexual differentiation, and the male gonad, therefore, starts to function as an endocrine gland before the female gonad to which the cortical layer is added somewhat later.

Whether male or female sex organs begin to develop in the early embryonic stages is conditioned by the chromosomal make-up. There is apparently no real sex differentiation, however, until after the primordial sex tissue has been laid down in the embryo. The male organs of reproduction have their homologues (similarity of origin, not function) in the female and vice versa (penis and clitoris or uterus and uterus masculinus, etc.); in other words, the primordia for both sexes are present, the make-up of the chromosomes being the determining factor as to which will begin to develop, the full development in turn being conditioned by hormones secreted by testicles and ovaries.

Sex is, therefore, determined by the genic balance, and actual differentation is brought about by the sex hormones. That the chromosomes or genes are not of themselves able to bring about sex differentiation in the higher animals is well-illustrated by the results following castration (or spaying). If castration of mammals is performed soon after birth, the two differently sex-determined classes, male and female, tend to remain the same; *i.e.*, sex differentiation does not ensue. The castrates have the sex genes XX or XY in all the cells of their bodies, but male or female secondary sex characters do not develop in the absence of the gonad hormones (see Chaps. IV and V).

Sex Reversal.—Sex reversal has been produced experimentally in several lower forms of animals. In the toad, for instance, there is a rudimentary organ, composed of rounded cells that resemble egg cells, located at the anterior end of the testicle. This is known as *Bidder's organ.* If the testicles of a young male toad are removed, the organ of Bidder will develop after 2 or 3 years into an ovary that secretes viable eggs. In other words, castration in this species throws the sex clear over to its opposite. Experimental work has also demonstrated that, in poultry, removal of the functional left ovary from a young chick causes the bird to develop the sex plumage and characters of the male, though it eventually returns to its original character. This is apparently due to the fact that the rudimentary right "ovary," in the absence of the suppressing effect of the ovarian hormone, develops into a testislike organ with seminiferous tubules in which some investigators report normal spermatogenesis. Occasionally, reports are circulated concerning hens that have changed into roosters and actually sired offspring, and the case reported by Crew is apparently an authentic case of sex reversal in the fowl.

In the higher mammals, sex is established at time of fertilization, and sexual differentiation begins fairly early in embryonic development. The young embryo has the primordia for either sex, and its genetic make-up determines which one will develop. The mechanism, genic, hormonal, environmental, sometimes fails to function perfectly and pseudohermaphrodites are produced. These are of various sorts; *i.e.*, both the male and the female embryonic primordia have developed to varying degrees from slight variations from one sex or the other to practically equal development of both sexes, but perfect in neither. Pseudohermaphrodites are more numerous in goats and pigs than other farm animals, and a few cases are known in man where one gonad developed into a testis found in the scrotum, the other into an abdominally located ovary. The external genitalia are also abnormal. Whether these aberrations are genetic or developmental is generally difficult to determine, but many no doubt do have a genetic basis.

Complete functional sex reversal following birth in the higher animals is unknown and practically inconceivable. Embryonic sex reversal, *i.e.*, hormonal or environmental influences completely reversing the gene-determined sex of an individual, is perhaps thinkable but has never been demonstrated.

Conditions Influencing Sex Ratio.—With sex evidently determined by the interaction of genes in the sex chromosomes and others in the autosomes and with one sex or the other (varying in different species) being heterogametic, we would expect generally to find an equality of numbers between the sexes provided there is equality of numbers and viability of the heterogametic sex cells, no selectivity between germ cells of the two types, and no differential embryonic mortality between the sexes. Nevertheless, the sex ratio is not always 1:1. Variations from the numerical equality of the sexes may conceivably be due either to genetic or environmental causes.

Genetic variations have been found in Drosophila. One of these behaves as a sex-linked and sex-limited-to-male gene that, when present in a male, either prevents the Y-bearing spermatozoa from being formed in numerical equality or lowers their ability to reach and fertilize the egg, for the offspring of such males have 96 female:4 male offspring. Even in the homozygous form, it apparently produces no ill effect in the female. Various lethal and semilethal sex-linked mutants are known in Drosophila, some of which kill only the females, because the Y chromosome carries the normal allele. Lethals in the autosomes sometimes give rise to peculiar sex ratios. In some interspecific crosses, no males or a greatly reduced number is born; in others, the reduction comes in the females.

Environmental conditions are also known that have an influence on the sex ratio. Seiler has shown that temperature affects the extrusion or retention of the X chromosome in a moth (*Taeloporia tubulosa*) in which the female is heterogametic. Season of breeding has been reported by many authors to have an effect on the sex ratio produced, as have also time of breeding during heat, age of parents, etc., but these contentions are not well-supported. Jull reports a sex ratio in poultry based upon annual production of 48.41 ± 0.47, and for the normal hatching season, March and April, of 48.82 ± 0.80. The same investigator also furnishes the following table:

TABLE 38.—SEX RATIO OF PULLET EGGS FOR EACH SERIES OF 20 EGGS

EGG PRODUCTION	SEX RATIO[1]
0– 20	62.91 ± 1.44
21– 40	57.46 ± 2.88
41– 60	45.00 ± 2.04
61– 80	44.61 ± 0.69
81–100	37.65 ± 1.00
101–120	32.53 ± 1.15

[1] This sex ratio is based on fifty females (from Jull).

It will be seen from the foregoing table that an early tendency in pullets to produce a preponderance of males gradually shifts over, as egg laying proceeds, to a tendency to produce a preponderance of females. Discussing these results Jull says:

Since in the domestic fowl the male is homozygous for sex, it does not seem probable that the spermatozoa would influence the situation. It is apparent that increased egg production must bring about certain changes in the eggs, so that more and more females are produced as egg laying advances. There was no indication of sex reversal, since a positive check was used to test this possibility. Brown Leghorn males were mated to barred Plymouth Rock females and the male progeny were barred and the female progeny were black. All the available evidence points to the conclusion that the different sex ratios occurring in the different periods are due to differential maturations in the egg. Apparently, among the first eggs laid the female-producing chromosome complex is extruded as a polar body more frequently than the male-producing complex, and as egg laying continues the male-producing complex tends to be extruded as a polar body more frequently than the female-producing complex. This tendency for the extrusion of one kind of chromosome complex in preference to the other at different stages of egg production is probably due to differences in the chemical composition of the eggs in early as compared with late laying. The differences in the chemical composition give rise to different reaction systems within the reproducing cell.[1]

[1] JULL, M. A., Can Sex in Farm Animals Be Controlled, *Amer. Soc. Anim. Prod. Proc.*, 96 pp., 1922.

Results somewhat similar to those of Jull were obtained by Hays in an experiment to test the effect on the offspring of very frequent service by the male rabbit. In this species the male is heterogametic and just as with Jull's poultry, where the increased functional activity of the ovary tended to produce a swing to a lower sex ration, so also with Hays's rabbits the increased functional activity of the testicle tended to produce a swing to a lower sex ratio.

The following tabulation makes this clear.

	Service				
	First	Fifth	Tenth	Fifteenth	Twentieth
Sex ratio	56.33	43.50	44.44	34.64	21.87

Hays offers two explanations of the foregoing lowering of the sex ratio: (1) that there may be an increase of female-producing spermatozoa as the burden of service increases, (2) that the male-producing spermatozoa become weaker with increasing service. The second explanation seems the more probable, because the increased functional activity of the secreting tissue of the testicle could very well bring about, through its chemical processes, a changed rate of metabolism. The explanation in both fowl and mammal is to be sought in terms of the chemistry of the ovaries and testicles—in other words, it probably is metabolic.

Effect of Selection on Sex Ratio.—King's work with the albino rat illustrates the way in which selection may influence the sex ratio. This investigator, starting with two pairs of rats from the same litter, inbred litter brother and sister for 25 generations. With no selection from a sex standpoint in the first six generations, the sex ratio was 108.6, compared with a norm of 105. After the sixth generation, selection was made along two lines, *viz.*, the *A* line taken from litters with an excess of males and the *B* line taken from litters with an excess of females.

The sex ratios were as follows:

TABLE 39.—SEX RATIOS IN KING'S INBRED RATS

A-line female × *A*-line males	122.3
B-line females × *B*-line males	81.8
A-line females × stock males	115.6
B-line females × stock males	91.1
Combined data for the two inbred lines	102.7
Stock females × *A*-line males	102.3*
Stock females × *B*-line males	96.2*

* Not significant statistically, according to King.

These results indicate that the sex ratio may be changed by selection, inasmuch as the straight inbred lines *A* and *B* differ from the norm by 17.3 and 23.2 points, respectively, but no wholly satisfactory explanation of the results has been devised. Miss King suggested that they might be due to differences in chemotactic attractions between ova and spermatozoa. Differential mortality rates between the two types of spermatozoa or the embryos arising from them might also be involved.

Any livestock breeder can cite instances of certain individuals, both male and female, that have tended to produce offspring preponderantly of one or the other sex. At the National Dairy Show in 1923, there was exhibited Financial King's Interest, a twenty-three-year-and-nine-month-old Jersey cow that had produced 21 calves, 20 heifers, and 1 bull. The records at the Massachusetts State College show a Guernsey bull that left 28 bulls and 14 heifer calves, a Holstein that left 26 bulls and 19 heifers, an Ayrshire that left 18 bulls and 7 heifers, and a Jersey that left 11 bulls and 6 heifers. These are the most extreme cases that can be found in this dairy herd over a period of about 15 years. Among the cows 3:7, 2:6, 7:0, 7:1, and 7:2 combinations are the most extreme. The cows, as a whole, have produced 471 male and 452 female offspring.

Whether the tendency to produce more males or females runs in families, *i.e.*, has a genetic basis, has not been proved, and, if it were proved, the introduction of another male might lessen or reverse the tendency. A breeder is often faced with the practical problem of having a male that seems to sire a preponderance of male offspring, a bull that sires 16 bull calves in a row. Shall the breeder sell this animal and try again, or is the tide about to turn toward a sequence of heifer calves? There seems to be no categorical answer to this problem, and as in so many other situations in breeding the only method is that of trying, and the best answer that of experience.

Conclusions Regarding Sex Determination.—The work herein reported seems to justify the conclusion that, in mammals, sex is determined by the type of spermatozoon that fertilizes a given ovum, and the paucity of knowledge concerning the factors that determine just what spermatozoon shall fertilize a given ovum must be admitted. It may possibly depend upon the chemical attraction between spermatozoa and ova. Those who argue that sex is dependent on the male are partly right, because the germ-cell differentiation in mammals occurs in the male; and those who argue that sex is dependent on the female may be partly right, because the ovum may possibly attract some spermatozoa more strongly than others. Unquestionably, chemical changes that affect the sex ratio do occur in both spermatozoa and ova, and the solution of the problem will result from a more thorough knowledge of both sexes, as, no doubt, they both exert large influence.

Sex Control.—As stated in the introductory paragraph of this chapter, a great many theories for the way in which sex is determined have been proposed. Genetic and cytological evidence, as well as logic, support in full the notion that sex is determined, as are all other potentialities, by the genes. In mammals the male is heterogametic, and what determines whether one or the other type of sperm shall fertilize the egg is unknown.

Many ideas have also been advanced as to the ways in which the sex of the offspring might be controlled. One theory is that service early in the heat period will result in a preponderance of male offspring, late in heat a preponderance of females. Another theory is based on the notion that one ovary produces male-producing eggs, the other female, and that the ovaries alternate in the liberation of eggs. A patent for a sex calculator based on this erroneous notion has been granted by the U.S. Patent Office. Still another theory holds that an alkaline vaginal reaction favors the production of males, an acid reaction the production of females. This and many other theories need further experimental testing under rigidly controlled conditions.

This problem of controlling the sex of the offspring is apparently a problem in devising means to separate the two types of sperms in mammals or to inactivate one or the other type.

Thus Koltzoff and Schroder have tried to separate the Y- and X-bearing spermatozoa by passing an electrical current through a sperm suspension. Rabbits were used for the experiments. One doe artifically inseminated by sperm from the anode produced six young, all of the female sex. Another doe was impregnated with sperm from the cathode, and produced four male and one female young, while a third doe impregnated with sperm from the central part of the tube produced two male and two female young. These results are very meager but the authors consider it improbable that they were due to chance alone. Repetition of the experiment on a larger scale is greatly to be desired.[1]

It seems highly probable that through the aid of physics, chemistry, possibly serology, immunology, and the device of artificial insemination, one may eventually be able to bring about the production of males or females at will. From a breeding standpoint this would have very marked advantages over the present system of trusting to luck.

Summary.—The general role of the chromosomes in the determination of sex was substantiated in 1905. The two principal additions to the chromosomal theory since that time have consisted of the theory of "genic balance" between the autosomes and sex chromosomes and the more recent localization of the effective materials in the sex (X) chro-

[1] Cole, L. J., and Johansson, I., Sex Control Again, *Jour. Hered.*, **24** (7): 273, July, 1933.

mosome to a known small region of this chromosome. We have lately come to understand more fully the part played by the endocrine secretions in sex differentiation among the higher animals as well as some of the conditions that affect the sex ratio and the possibilities of affecting the latter by selection. In spite of many attempts to solve it, the problem of controlling sex remains unsolved up to the present.

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[1] See lists at end of Chaps. XII and XIII.

SECTION IV

The Art of Breeding

CHAPTER XX

SYSTEMS OF BREEDING—UNRELATED ANIMALS

We have now completed three sections of this text on animal breeding. The first section was designed to give the student an over-all view of the history and status of breeding at the present time as well as an introduction to the origin and relations of all living forms in terms of the probable physical basis of life and inheritance—the genes and chromosomes.

The second section dealt with the scientific and practical phases of reproductive physiology in order to acquaint the student with the fundamental procedures in the production of a new generation and to indicate the practical procedures that will best ensure a high degree of reproductive efficiency.

The third section dealt with the workings of the genes and chromosomes in the perpetuation of similarities and the creation of new types among related forms. Perhaps the student sometimes wondered why he should learn all the details of mono- and dihybrid crossing, of dominance and epistasis, of lethals, multiple alleles and multiple factors, of sex-linked and -limited inheritance, of linkage, crossings over, chromosome mapping, interference and limitation of the linkage groups, and of the various and sundry types of gene mutations and chromosomal aberrations, for it is so difficult to find examples of the actual working of these principles in the farm mammals. Knowledge of the basic principles, nevertheless, should be valuable in acquainting the student or breeder with the complexity of the problem with which he is dealing. He can rest assured that all of these principles are at work in the germ cells of the animals in his herd or flock, although in most instances so many genes are involved and so few offspring are produced that the result of the operation of any one principle is generally difficult if not impossible to measure.

Such knowledge should also make the breeder approach his practical problem of creating better animal types in a less cocksure manner and with a greater realization that he is dealing with a complicated mechanism which demands as full a knowledge of details as it is possible to achieve.

In rebuttal, it might be argued that old-time breeders often achieved great success in total ignorance of the basic principles. This must be admitted, but we should be aware of the fact that less publicity has been given to those old breeders' more numerous failures. Their task was to create a few outstanding individuals, which they did; ours is to raise the average merit of all our animals, which can be accomplished only if we fully understand the natural principles underlying reproduction and the mechanics involved in hereditary transmission.

This, the fourth and concluding section, will deal with the practical applications of the general principles outlined in Sections II and III in the breeder's task of stimulating new and helpful variations and then holding the gains that he has made.

Each breed of livestock, as now constituted, has as its genetic capital the complete reservoir of genes as they exist in the living members of the breed. Each breed has a certain number of good genes and a certain number of bad ones. If the number of good genes can be increased at the expense of the bad ones, the breed will progress. If the opposite result eventuates, the breed will retrogress.

The breed is debarred by its own rules from going outside of its own limits for new genes. It cannot hope for any speedy progress from the natural occurrence of beneficial gene mutations, and there is at present no known way of creating helpful mutations through artificial means. Breed progress depends, therefore, on the relative gains in frequency of its desirable genes and possibly their recombination into more desirable groupings. New breeds can also be created, if and when that seems desirable or necessary, by combining characters, as they now exist in separate breeds, through systems of crossbreeding and selection followed by inbreeding.

An individual breeder, likewise, has as his genetic capital the genes existing in his living animals. He, of course, can augment this supply by purchase from other breeders. He usually does this through the purchase of males.

Before the breeds were formed as such and their books closed, a group of breeders in a region could and did go outside the not too distinct confines of their own type to get some genes that they desired. In getting these good genes, they also had to take some that they did not want. Their task was, therefore, that of so mating and selecting their animals that they might retain the good and discard the bad genes. It was in this fashion that our purebreds were formed.

The pool of genes in any breed has in general seemed to be elastic enough to permit the ideal to range between rather wide limits. At the beginning of this century the commonly accepted type of hog was short-legged, deep-bodied, and extremely rapidly fattening. Differential

growth rates exist between the various parts as well as tissues of the body. In this "chuffy" type of hog the bone growth and muscle growth proceeded rapidly to their rather low upper limits, whereas the third phase, that of fat deposition, came into play early and had a high limit. The result was an early maturing fine-boned animal with a high proportion of fat to lean. This type of growth was highly favored also by the prevalent practice of feeding largely on corn. The consumer demand gradually shifted to a leaner type of animal. To meet this changed demand, breeders changed their selection ideal as well as their system of feeding. By the late twenties or early thirties, the selection ideal in hogs had shifted to the other extreme—that of an upstanding, rangy, relatively shallow-bodied, and lean type of animal. In these animals the bone- and muscle-development phases continue for a long time and have a high upper limit; the fat-deposition phase arrives late and has a low limit as compared with hogs of the early 1900's. Probably, if a group of breeders of "chuffy" hogs in 1900 had been shown a picture of the "racehorse" type of 1930 and told that their job was to create such a type, their first reaction would have been, it can't be done. Due, however, to the facts that the market demanded the change and that the kind of genes necessary to produce such a change existed in the gene pool of all the breeds, the change was brought about in a remarkably short time.

Some physiological changes are very complex in their nature; they undoubtedly depend on the actions and interactions of a great many genes that probably act in large measure through the mechanism of the endocrine glands; and for their full expression they are dependent upon the environment, especially its nutritional phases. Similarly, the pool of genes in our present big type hogs undoubtedly contains enough of the genes for "chuffy" type to permit the reverse of the above-described change from "chuffy" to big type to be brought about should it ever be desirable to do so.

Another familiar example is the smoothing up of the type of our dairy breeds during the past 20 years. While average production has been improved, a far greater change has ensued in type also during this time. Some might and do argue that most or all the change in production has been due to better feeding and management. This argument cannot be used to explain the change in type. Again it is evident that the pool of genes in the various breeds contained a sufficient supply of genes making for smoothness of topline, proper set of legs, body, and udder capacity, and general quality so that conscious, directed selection for these things could be successful.

In one of our dairy breeds the byword among breeders 20 to 30 years ago was "the 30,000-lb.-of-milk cow." In practicing such selection the

genes making for higher fat test were automatically discarded, owing to the general negative correlation between high amount of milk and high butterfat test. But again there was seemingly enough of a supply of genes for higher test left in the general gene pool of the breed to make possible the raising of the butterfat test of the breed by at least one-half of 1 per cent.

One of our breeds of cattle has followed two divergent lines of development, one for milk, the other for beef. The genes for beef are still present in the former and those for milk in the latter, so that these two strains could be made to mutually replace each other if there were any point in doing so. Similarly, it would still be possible to make any beef breed over into a milking breed and vice versa by means of selection and systems of breeding.

With the actual formation of the breeds and closing of the books, the door to the admission of new genes, except such as might occur naturally through gene mutation, was closed. From that point on breed progress became simply a question of manipulating gene frequencies.

The technique for doing this resides in selection. The breeds or breeders try to increase their stock of good genes by permitting those animals which have the greater number of good genes to leave many offspring while restricting the number of offspring of those which have relatively few good genes. The first task of a breeder becomes, therefore, that of devising methods for ascertaining the sort of genes which his animals possess. This calls for some sort of measurement and for record keeping.

In addition to selection the breeder has the use of the tool of breeding systems.[1] Some systems of breeding render the germ plasm more heterozygous, others make it more homozygous. Both selection and systems of breeding can be used to influence gene frequencies, and they are the only means available for doing so. Systems of breeding and selection are the most important problems with which the breeder must deal. They constitute the art of breeding.

It should be understood at the very beginning that there is nothing about any system of breeding which guarantees it to be a success, or, on the other hand, that foredooms it to failure. Popular articles sometimes portray the systems of breeding used by some breeder or the type of matings used to beget some champion with the implication that similar methods should be adopted by all and sundry. However, the fact that some successful breeder used linebreeding has no necessary application to any other herd or flock.

[1] The term *systems of breeding* is here being used in a somewhat restricted sense. Constant selection is a breeding system as are also assortative and disassortative matings.

The success or failure of any system depends entirely on the genes present in the animals concerned, plus of course the breeder's ability to mate and select intelligently.

All systems of breeding can be grouped under two categories, *viz.*, outbreeding and inbreeding. The latter includes linebreeding and closebreeding, the former includes grading, the various types of crossbreeding and outcrossing. This chapter will be concerned with the various kinds of outbreeding.

Grading.—Breeds of animals arose by slow degrees from the general population of livestock by a process of selection. Along with better fleshing, milking, or other qualities, certain breed trade-marks such as color of hair or wool, shape and set of horns, etc., were secured. By systems of mating (often involving quite close breeding) and a continuous discarding of animals that did not show the desired combination of characters, animals which would breed relatively true were finally created. When this had been accomplished, the obvious best thing for the breeder without purebreds to do was to secure a purebred sire to use on his grade animals. Thus the breeding system known as *grading* came quite naturally into being.

Grading is the practice of using purebred sires of a given pure breed on native or grade females. Its purpose is to develop uniformity and to increase productivity and quality in the offspring. The pure breeds are generally capable of producing these results because they have been selected for many generations for particular points and purposes within rather narrow limits and specifications. This does not mean that a purebred will necessarily effect an improvement when bred to grade animals, for, unfortunately, as is quite generally recognized, there are even at the present time a goodly number of inferior purebreds. The average purebred, however, will help to bring about uniformity and to increase productiveness in the average grade herd and can be used for this purpose. The first-generation offspring will carry 50 per cent of pure "blood." When these in turn are mated to another purebred sire of the same breed, the resulting offspring will carry 75 per cent of pure "blood," etc. After five or six top crosses of this sort, where one breed has been adhered to for the sires, the animals are, to all intents and purposes, purebred, though they are not eligible to registration. This is because the purebreds have certain definite distinguishing characteristics that breeders do not want to see disturbed. Such might occur if five or six top-crossed grade animals were admitted to registry, it being possible and probable that the grades would be carrying along some genes in their germ plasm for undesirable characteristics from the standpoint of the pure breed which would, at some future time, crop out in the breed.

As the amount of pure "blood" approaches closer to 100 per cent, the grades come to look and behave more and more like purebreds, and they finally come to be practically indistinguishable from them. A native female has 100 per cent grade genes. Her offspring by a purebred sire has had one-half of its grade genes replaced by purebred genes. If one of these first-generation grade females is in turn mated to a purebred sire, its offspring will in turn have had one-half of its remaining grade genes (50 per cent of those it has) replaced by purebred genes, etc. We, therefore, would expect the greatest improvement in the first cross and less in each succeeding generation as the number of purebred genes is increased. In addition, it has been observed that the bringing together of diverse genetic material often results in added vigor in the offspring. This phenomenon is called *heterosis*, and it would obviously be most noticeable in the first cross.

The fact that some grade animals outdo some purebreds has a tendency to lead some people to the erroneous conclusion that grading is better than pure breeding. Some purebreds have the genes that give them the external trade-marks of their breed but few of the genes for efficient production. Grading with this sort of purebred will not lead to rapid improvement, whereas grading with purebreds that have not only the external trade-mark genes but also a goodly supply of those causing efficient production will lead to rapid improvement. The majority of our animals are produced by grade breeding and probably will continue to be, as long as the average merit of the purebreds continues to excel that of the average commercial herd or flock. Here lies the real challenge to the purebred breeder to devise ways of ascertaining just what genes his animals do possess and also the means and the courage to rid his stock of poor genes.

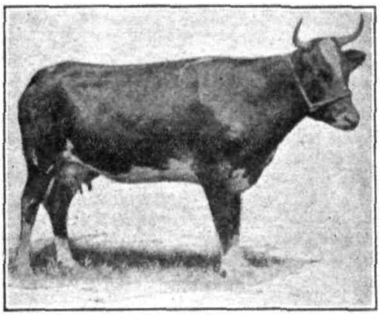
One of the principal functions of the pure breeds is that of serving as a source of seed stock for commercial producers. The commercial producer depends upon the purebred breeder to supply him with concentrated doses of good genes, which in turn means that the principal task of the purebred breeder is that of ridding his stock of poor genes. With such a double-barreled system in full operation it would seem logical to advise the average man starting in the livestock business to start with the system of grading. It will be admitted at once that this system leaves something to be desired, but it must also be admitted that it has its advantages. The most important consideration is, no doubt, that of cost. With grades, a start can be made for considerably less money than would be required for purebreds. Breeders of purebreds recognize that this practice is sound and advantageous to them, for it will furnish a market for all of a breeder's really meritorious males and for his relatively few excess females, most of which he will need to keep

and test. It will mean more business eventually for breeders of purebreds to have beginners start with a grade herd and a purebred sire and later, when they have learned something of the business and have become established, change over to a purebred basis. If beginners are induced to start with purebreds, the herd must be a small one because usually the capital at hand is limited and the opportunity for eventual success and growth in the business is thereby greatly curtailed. Many men have started with purebreds, have soon become discouraged, and either have gone back to grades or have gone entirely out of the livestock business. Besides the greater initial cost of starting with purebreds, there is another influence to consider, *viz.*, that when a man has invested in purebreds, he is quite likely to think that he ought either to sell all of his herd increase at rather high prices or to retain it in his own herd as breeding stock. This is an element that hurts the purebred breeding business in many ways. In the first place, all the increase of these herds is not capable of improving the breed, and a part of it should go to the packer. The average man will not hesitate to send surplus offtype or low-producing grade offspring to the butcher, but it takes more courage than some men possess to see the offspring of purebreds, for which they have paid considerable money, going that way. For purely commercial purposes, a herd of good grade animals, headed by a good purebred sire, is just as efficient and will make the owner as much money as a herd of purebreds.

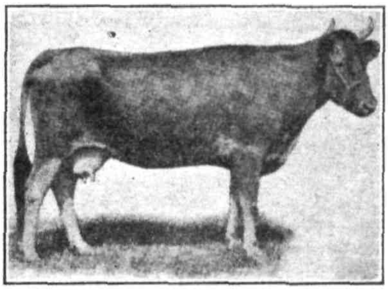
For the young breeder, it is a serious question whether to start with purebreds or grades. Many arguments can be advanced on both sides, and in the final analysis it is a matter to be settled individually. It would no doubt often be possible to start with somewhat old, timeworn purebreds about as cheaply as with grades. A prospective breeder might find that he could secure individuals that were growing old, cows with only three good quarters, etc., for the same prices he would have to pay for grades. If such animals were of good blood lines, had no hereditary defects or unsoundnesses, had a reasonable prospect of producing a few more offspring, and could still produce enough so that they would yield a little more than the cost of their keep, they no doubt would prove to be profitable investments. Young breeders of limited means who plan eventually to have purebreds may well consider this and somewhat similar plans for getting good "blood" (good germ cells) at reasonable prices.

McCandlish, Gillette, and Kildee, at the Iowa Agricultural Experiment Station, graded up a herd of scrub cows with purebred sires of the dairy breeds. The first-generation grades produced 55 per cent more milk and 44 per cent more fat than their dams, and the second-generation grades produced 116 per cent more milk and 106 per cent more fat than

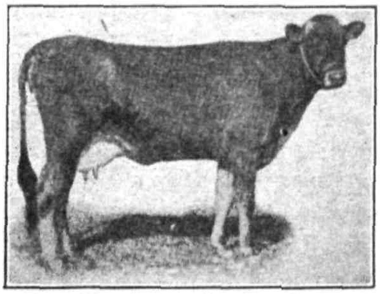
their scrub granddams, owing to the fact that these cows not only produced more milk, but had longer lactation periods, things for which the purebreds have been selected for a great many generations. The champion gelding at the International Livestock Exposition in 1921 and 1923, Major MacFarlane, was a grade horse two generations removed



Scrub cow No. 60. Average production 3,313.2 lb. of milk and 178.47 lb. of fat.



Half-blood Jersey No. 241 out of scrub No. 60. Average production 6,126.4 lb. of milk and 348.98 lb. of fat.



Three-quarter blood Jersey No. 348 out of half-blood Jersey No. 241.

FIG. 125.—Showing results of grading up. (*From Iowa Agr. Exp. Sta. Bull.* 188.)

from a cayuse or Indian pony mare. The thousands of purebred beef bulls that have been used on the cattle of the Western ranges during the last half century have graded up these herds and greatly improved the quality of the carcasses produced. It is in this field, the grading up of the common herds and flocks, that scientific breeding and farsighted

breeders can wield a great influence. The government's recent purebred-sire campaign has been very well received by breeders and farmers and will doubtless greatly increase the average and total value of livestock in the United States.

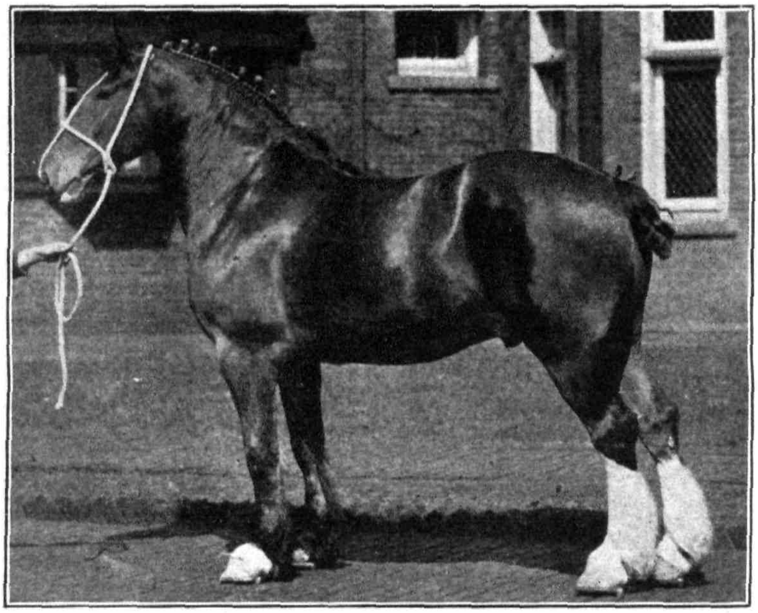


FIG. 126.—The grade Clydesdale gelding, Major MacFarlane, champion at the International 1921 and 1923. He is only two generations removed from a cayuse mare.

The following is the summary and conclusions following 10 years of grading up beef cattle at the Sni-a-Bar ranch in Missouri:

The use of purebred sires of acceptable quality results in successive improvement in the quality of the calf crop, as shown by conformation and market price.

The greatest single step toward improved quality, compared with common stock, occurs in the first cross. Subsequent crosses increase quality and market value still more, though in less marked degree.

Quality and best market prices are approximately in proportion to the number of crosses of pure breeding.

After the third or fourth cross the offspring compare very favorably with purebred stock in conformation, and only exceptionally good sires can bring about further improvement.

Steers sired by purebred bulls at Sni-a-Bar Farms have topped the market 16 out of 20 times and have 4 times been the highest for the year to date of sale on the Kansas City market for fat yearling beeves.

Early maturity is a conspicuous result of beef-cattle improvement through the use of purebred sires.

Steers raised at Sni-a-Bar Farms as a part of the demonstration have sold consistently for about $2 a hundred pounds more than the average of other cattle on the same market, and during the period of high prices in 1918 for as high as $5.95 a hundred above the market average.

Show-ring results are in general agreement with market preferences so far as indicated by the successful showing of Sni-a-Bar stock in market classes and by sales of similar cattle on the market.

The demonstration shows clearly that breeding is a dominant factor in the production of high-quality beeves and that good feeding and management will not return best results unless the element of good breeding is present also.

In grading up farm cattle the quality of calves is approximately in proportion to the individual excellence of the sires used, hence the importance of selecting bulls possessing qualities sought for in the offspring.

Attendance at the grading-up demonstrations has increased from about 500 persons in 1917 to 10,000 in recent years, indicating a wide public recognition of the practicability of raising better cattle.[1]

Crossbreeding.—Crossbreeding includes several types of matings. Most generally the term means the mating of purebred animals belonging to different breeds. It sometimes is used to cover the mating of animals belonging to different species, *e.g.*, the horse and ass cross resulting in mules and hinnies, but this might better be called *hybrid breeding*. Again the term *crossbreeding* is used to cover cases of mating purebred sires to high-grade females, but this actually is grading.

Crossbreeding brings together more or less divergent sorts of germ plasm, which gives rise to variations, especially in the F_2 and subsequent generations. In this, as well as in the matters of size, vigor, and fertility, one or more of which crossbreeding usually increases, it is quite often the opposite of close breeding. Crossbreeding has both desirable and undesirable features.

Crossbreeding is used to a considerable extent in the production of meat animals, because crossbred animals usually show an increase in growth and vigor over either one of their purebred parents. The exact cause of this phenomenon is not known, though some authorities suggest that it may be due to the fact that all breeds or varieties carry in the germ plasm, along with their desirable genes, some inhibiting genes, and that in crossbreeding these inhibiting genes in each species or breed are neutralized by genes from the other species or breed. The term given to this feature is *hybrid vigor*, or *heterosis*. At any rate, it is proved that the animals resulting from such crosses are usually more vigorous. The mule is highly prized for this very feature, being tough, vigorous, hardy, and because of its lighter weight the mule requires less feed for maintenance than the horse. Generally speaking, the mule is not quite

[1] *U.S. Dept. Agr. Misc. Cir.* 74, pp. 26–27, 1926.

so fastidious as the horse, but when properly treated and trained, it is fully as tractable and serviceable. Some of the grand-champion steers at the International Livestock Show have been crosses among Herefords, Angus, Shorthorns, and Galloways. California Favorite, the grand champion in 1916, was a crossbred Shorthorn-Hereford and was reputed to have been one of the finest steers ever exhibited.[1]

Crossbred animals are generally superior in individual merit if the cross proves to be a desirable "nick," but their breeding merit is also

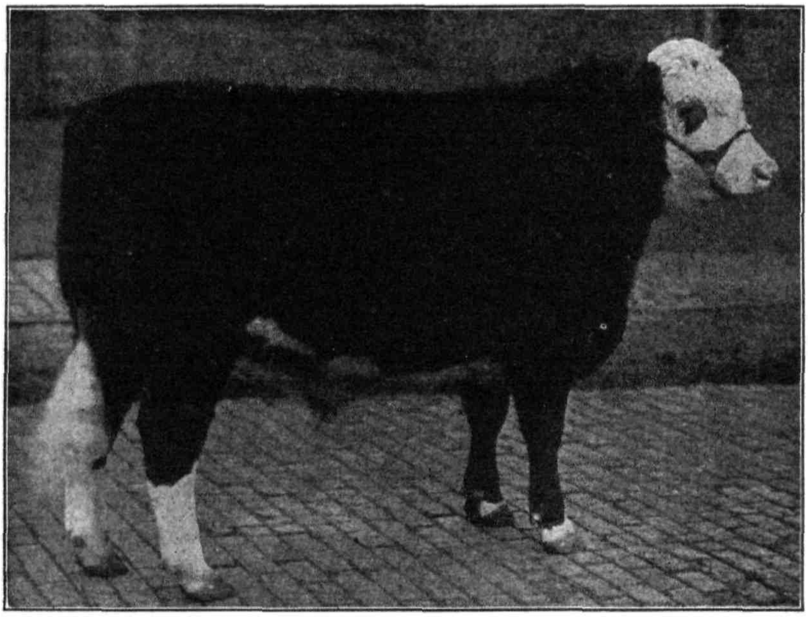


FIG. 127.—California Favorite, the Grand Champion steer at the 1916 International Livestock Exposition. The steer was out of a red Shorthorn cow and by a Hereford bull. (*From Babcock and Clausen, Genetics in Relation to Agriculture.*)

generally reduced because of the heterozygous nature of their genes and the fact that all animals transmit only a sample half of their own genetic materials to their offspring. The result is that the favorable gene complexes that make any breed successful are broken up, and various assortments of genes from both the breeds are passed on by the crossbreds to their offspring.

A great many crossbreeding experiments have been carried out during the past 30 years. They indicate that both the sire and the dam have, speaking generally, equal influence upon the offspring, though, of course, either parent may be more or less prepotent for certain characteristics. In March, 1924, a double litter of pigs was born at the farm of the College

[1] A crossbred Shorthorn-Angus won in 1941.

of Agriculture of the University of Illinois. It was a double litter in that a Duroc-Jersey sow was mated to both a Duroc-Jersey and a Poland-China boar at one estrus. The resulting litter contained 10 pigs, 6 of which were Duroc-Jerseys, whereas the other 4 were spotted red and black and therefore evidently crossbreds sired by the Poland-China boar. The purebred pigs weighed 3.23 lb. each at birth, whereas the crossbreds averaged 3.75 lb. The pigs were all handled and fed in the same manner and at six months the 2 remaining purebreds (females) averaged in weight 185.5 lb., whereas the 4 crossbreds averaged 235.2 lb. and the 2 female crossbreds averaged 228 lb. This is a striking example of heterosis.

Crossbreeding between Chester White and Yorkshire swine at the Bureau of Animal Industry Farm at Miles City, Mont., is summarized in Table 40.

TABLE 40.—PUREBRED-CROSSBRED COMPARISON*

	Litters	Pigs	Weight, birth	Number weaned	Weight, 70 days	Daily gain	Feed, 100-pounds gain
Purebred Yorkshires	38	10.6	2.40	7.6	38.4	1.21	375
Purebred Chester Whites	36	9.8	2.38	6.6	39.4	1.30	403
York. male × Chester White female	29	9.9	2.49	7.4	42.7	1.35	371
Chester White male × York. female	29	10.1	2.42	8.0	42.8	1.33	370

* From *Iowa Agr. Expt. Sta. Bul.* 380.

If we average the above figures for the purebreds and for the crossbreds we find that the crossbreds weaned 8 per cent more pigs which weighed 11 per cent more at seventy days and gained 7 per cent more per day up to market weight on 5 per cent less feed than the purebreds.

The Iowa Experiment Station reports as follows on 108 litters of crossbred pigs from the Duroc-Jersey, Poland-China, Yorkshire, and Landrace breeds: (1) fewer stillborn pigs, (2) crossbreds more vigorous at birth and more reach weaning age, (3) crossbreds 3 to 4 lb. heavier at weaning, (4) crossbreds gained 0.09 to 0.12 lb. more per day, (5) crossbreds saved 10 to 14 days in reaching a weight of 225 lb., (6) crossbreds saved 25 to 30 lb. of feed in reaching 225-lb. weight.

Crossbreeding for the Market.—Next to grading, crossbreeding is used most extensively in the production of meat animals including poultry. Its greatest use up to the present has been with swine, less with sheep, and least of all with cattle and horses. In cattle a small

amount of crossbreeding is practiced between Angus or Galloways and white Shorthorns to produce the blue-gray crossbred, between Angus and Herefords to produce black animals with white faces, as well as crosses between the beef and dairy breeds. Some beef ranches use a small proportion of bulls of another breed to utilize somewhat the principle of heterosis, whereas in some of the Gulf states a small proportion of Brahman blood is maintained in the cow herds to give added resistance to insects and disease. Crossbreeding has also been used in cattle for the purpose of studying the genetic mechanisms involved in the transmission of fattening and milking propensities.

Crossbreeding is also practiced quite extensively by range sheepmen by using rams of the Down breeds on grade Merino or Rambouillet ewes for the production of market lambs.

The most extensive use of crossbreeding has occurred with swine. The usual system is that of using purebred boars on purebred or high-grade sows of another breed. This generally results in the production of faster and cheaper gains. The disadvantage of this type of breeding is that sow replacements as well as boars of the other breed must be purchased, there being no opportunity for selection among the gilts, for the advantages of crossbreeding are soon lost if the crossbreds are used for breeding. If these crossbred gilts are used for breeding, their offspring are quite variable and generally not equal to their dams as individuals. It is thus impracticable to take advantage of the crossbred gilts' possible superiority in fertility and milking qualities.

Various attempts have been made to overcome this difficulty. Workers at the Minnesota Experiment Station have suggested a method known as *crisscrossing*. Sows of breed A are mated to a boar of breed B. Crossbred gilts from these matings are then selected and bred back to a boar of breed A, selected females from these matings being mated to boars of breed B, etc.

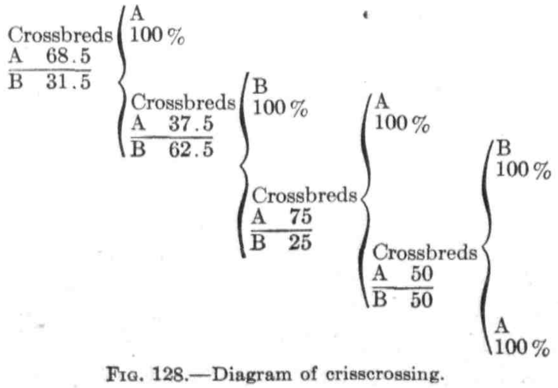


FIG. 128.—Diagram of crisscrossing.

It is seen from Fig. 128 that the crossbreds under crisscrossing soon come to have about two-thirds of their blood from the breed of their immediate sire and one-third from the breed of their maternal grandsire. The Minnesota Station reports:

The crossbred litters averaged from one-third pig to two pigs larger at weaning; on the average, each pig weighed from 5 to 7 pounds more at weaning, and the litters weighed from 39 to 96 pounds more than the purebreds. The crossbred pigs reached a market weight of 220 pounds from 17 to 22 days earlier than comparable purebreds, and they reached that weight on from 27 to 36 fewer pounds of grain.[1]

Another system of continuous crossbreeding involves the use of three pure breeds and is known as *triple crossing*. This is diagramed in Fig. 129.

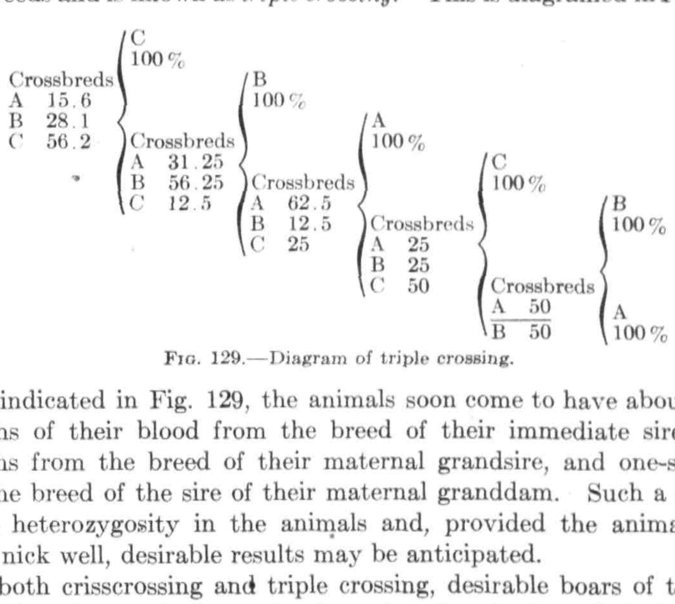


FIG. 129.—Diagram of triple crossing.

As indicated in Fig. 129, the animals soon come to have about four-sevenths of their blood from the breed of their immediate sire, two-sevenths from the breed of their maternal grandsire, and one-seventh from the breed of the sire of their maternal granddam. Such a system retains heterozygosity in the animals and, provided the animals and breeds nick well, desirable results may be anticipated.

In both crisscrossing and triple crossing, desirable boars of the two or three breeds must be located and purchased and unless all the breeding is to be done with the gilts, more than one boar must be maintained at all times. If the young sows go to market after having had but one litter, little constructive selection can be practiced. When this disadvantage is added to the extra cost of buying replacements, it seems questionable whether the generally less than 10 per cent advantage in rate and efficiency of growth in the crossbreds due to heterosis is great enough to warrant its wide adoption.

The rate of replacements will, of course, vary with different classes of livestock. With cattle the useful life of a cow probably averages

[1] *Minn. Expt. Sta. Bul.* 320.

between six and eight years, which means that 12 to 16 per cent of the cows must be replaced annually so that in a 100-cow herd even with 100 per cent breeding efficiency, which of course is seldom achieved, one-quarter to one-third of the herd would have to be bred to a purebred sire of the same breed each year and all the resulting females raised in order to provide replacements at home. With ewes the length of the useful life is less, probably four to six years, so that a still larger proportion of the flock must be bred pure each year, though this may be reduced somewhat if the percentage lamb crop exceeds 100. With sows the useful life is from four to five years, and, because they may be managed so as to produce six to eight pigs twice a year, the replacement problem is greatly simplified, for the replacements could be provided from one purebred litter each year.

Crossbreeding and New Breeds.—Crossbreeding with its attendant variation, plus later painstaking selection and inbreeding, has been used for the creation of several new breeds. In sheep, the Oxford Down is the direct result of crossbreeding, the Cotswold and Hampshire Down furnishing the pure breeds for the cross. This crossing, followed by rigid selection for specific points and type, has established the Oxford Down as a pure breed. The Corriedale, a New Zealand breed of sheep, resulted from the use of Leicester and Lincoln rams on Merino ewes, and the Columbia breed was created by the specialists of the U.S. Department of Agriculture, using the Lincoln and Rambouillet breeds. The Bureau of Animal Industry, at its Middlebury, Vt., experimental farm, is at present developing a new breed of sheep from crossing Corriedales and Southdowns to be known as the Southdale breed.

Two things should be borne in mind so far as the creation of new breeds is concerned. One is the fact that two men might start to cross breeds A and B to produce a new breed C. Since none of our breeds is entirely homozygous, they would surely start with different genetic materials. In addition, chance sampling of the hereditary material plus different ideals in each breeder's mind might result eventually in two samples of a new breed, called C, made up of very dissimilar genes and therefore very dissimilar in type and productive capacity. If they sold stock to other breeders, the two strains might further diverge. Just how much divergence is to be tolerated before they should be called separate and distinct breeds is a matter of admitting of various opinions. The other point to be kept in mind in the creating of new breeds is that of the time involved. Whether it is to take 6 generations or 16 or 60 before one would be justified in saying that the result of the original crossing and later selection now merits being called a purebred is also an arbitrary matter. Many of the so-called *new* breeds still show a great range of variation after 25 or 30 years of careful selecting, and, as

we have just stated, even the oldest of our pure breeds are still relatively heterozygous.

The King Ranch of Kingsville, Tex., has developed a new breed of cattle, the Santa Gertrudis, by crosses of Brahman cattle on Herefords and Shorthorns. These last-named beef breeds, which had replaced the native Texas and Mexican cattle, produced a better carcass, to be sure, but the herds suffered heavy losses from drouth and insect ravages, and the calf crop at times was very small. Brahman bulls were used on Shorthorn cows and these crossbreds mated. In this way a sire, Monkey, was eventually produced that, when bred to first- or second-cross hybrids, produced the Santa Gertrudis breed. "This cross (3/8 Brahman and 5/8 Shorthorn) seems to give the maximum of size, hardiness, and ability to fatten; the highest dressing percentage, resistance to heat and insect pests, and the practical elimination of the hump." Lamonia, a new breed of poultry, has recently been created by crossbreeding. Leghorn, White Plymouth Rock, and Dorking were the breeds used in founding Lamonia, which combines the characteristics of good production, a white-shelled egg, and desirable type for meat.

It should be possible through crossbreeding to establish new breeds with any desired combinations of characters, unless, of course, the latter are antagonistic to each other or certain genes are linked in such a way in the germ plasm that segregation is impossible. The drawbacks to this procedure are serious ones, however, because of the time and expense involved and the large number of animals that must be produced in order to give ample range for selection. After these difficulties have been overcome, there would still remain even a greater one, *viz.*, selling the new breed to the breeders and growers. The breeds as they exist today seem to fill most of the needs fairly well. Considerable variation still exists in all of our breeds, in fact, probably enough so that those in each of the classes could for the most part be made uniform in productive qualities through suitable matings and selection, although they would still differ in external character such as color, presence or absence of horns, set of ears, etc.

This whole matter of the possible creation of superior new breeds in any and all classes of livestock is an extremely fascinating one and has intriguing possibilities, though it is not a field in which an ordinary breeder with limited time, capital, and number of animals can hope to achieve success. He lacks the necessary equipment. If exploited at all, these fields should be left to the state agricultural experiment stations or the U.S. Department of Agriculture.

Various Commercial Hybrids.—The mule is at the present time the best known hybrid in the United States. The mule is the result of crossing a jack (male of the ass family) on a mare (female of the horse

family). This cross has been valued for many centuries. Fertile mare mules have been reported at various times, but the reports have not until recently been capable of absolute verification. In 1920, L. T. Branham of Montalla, Tex., reported that a mare mule in his possession, which had been bred to a jack, had dropped a living foal. The contention was supported by affidavits of the owner and some neighbors. The mare was loaned to the Texas Agricultural and Mechanical College and after failing to conceive when bred to a jack in 1921 dropped a living stallion colt in 1923 as the result of being mated to a saddle stallion the year previous.

Another fertile mule has been reported from Indiana.[1] When bred to a Percheron, she dropped a stud colt with no mule or ass characteristics. Still another fertile mule has been reported from Arizona.[2] This mule bred to a jack dropped a mule foal, and motion pictures were taken of the birth. This mule is said to have dropped one other foal previously. In the above, we have two cases of mare mules bred to jacks producing mule foals and two mare mules bred to stallions producing horse foals. Since the chromosome number in the ass family is thought to be somewhat larger than the 60 found in the horse, the inference in each of the above cases is that these mare mules occasionally produce an egg containing nothing but 30 horse chromosomes, all the ass chromosomes having been extruded in the polar body. These results indicate that these fertile mare mules actually function as mares as far as the genetics of their eggs is concerned. If all the horse chromosomes were extruded, these mules would function genetically as asses. No cases of this sort have yet been reported, and the possibility of securing a fertile hybrid strain of true-breeding mules is as remote as ever and would seem to be theoretically impossible.

The genetic pedigree of these offspring of mules illustrates the sampling nature of the hereditary process, for they should evidently be written

	Stallion or jack	Stallion or jack Mare or jennet
Offspring: Horse if by stallion Mule if by jack		
	Fertile mule (passed on nothing but horse chromoromes)	Stallion This line of pedigree obliterated genetically from this point back

FIG. 130.—Pedigree of offspring of a mule.

The mule approximates more closely to the ass than to the horse in general characteristics.

[1] See *Jour. Hered.*, p. 549, 1939.
[2] See *Jour. Hered.*, p. 548, 1939.

The hinny is the reciprocal of the mule, being the result of a stallion-jennet cross. It is said to more closely approximate the horse in general characteristics. The hinny has never become popular or numerous.

The zebroid, a zebra-horse hybrid, is fairly popular in the tropics because of its docility and its resistance to disease and the effects of the heat.

Several hybrids in the genus Bos are fairly common. Of these one of the best known and most valuable results from crossing the zebu, or humped variety of cattle (Brahman), on ordinary cattle. Heterosis is evidenced and the zebu's resistance to ticks, fever, and various diseases is at least partially dominant. This cross is quite common in Brazil and seems to be gaining in popularity in the Southwestern part of the United States, especially in Texas.

Bison and cattle belong to the genus Bos and are interfertile. Bison bulls are bred to domestic cows to produce this cross. Males are seldom born alive, owing either to their height back of the shoulders, which prevents their passing through the cow's pelvis, or to too great a quantity of amniotic fluid, and seem never to be fertile. Some of the females are fertile. The first cross, bison bull on domestic cow, is called a *hybrid* or *half-bred bison*. The second cross is made by using a domestic bull on the foregoing hybrid. The females resulting from this cross are mated to bison bulls and the offspring are termed *cattaloes*. Besides more rapid growth and greater vigor the following advantages over cattle are attributed to the cattalo, *viz.*, greater resistance to many diseases, including blackleg and Texas fever, higher dressing per cent, failure to run from heel flies and to drift in storms, lower feed requirement, and a greater ability to withstand lack of water.

Disadvantages of Crossbreeding.—Some of the disadvantages of crossbreeding have already been mentioned. If a man is to crossbreed, it means that he must keep two or more pure breeds in order to produce the crossbreds. This involves a considerable investment, as rapid progress need not be expected in any line of breeding unless sufficient numbers can be kept to allow for rigid selection. Another even more serious disadvantage in the field of crossbreeding is the fact that most breeders cannot resist the temptation to use some particularly good crossbred animal for breeding purposes. The crossbred may have all the distinguishing characteristics of a purebred, be capable of more rapid growth as well as being more vigorous, but no crossbred animal can behave as a purebred in hereditary transmission, because the crossbred animal, owing to the nature of its origin, cannot produce even a relatively uniform set of offspring, because it cannot produce a uniform set of germ cells. It will be recalled that determiners for the various characteristics separate or segregate out independently of each other, unless,

of course, they are located in the same chromosome, under which condition they tend to stay linked together. This independent segregation and recombination produces a wide range of variation—dissipates uniformity. Heterosis or hybrid vigor exhibited by crossbreds is not continued in future generations of their offspring.

Finally, we should mention the aesthetic side of the problem. We all know of the pride that the good purebred breeder takes in his uniform, trade-marked flock or herd, sometimes bordering on biased, prejudiced partisanship. "Belonging" to a pure-breed association gives many men a deep feeling of satisfaction, and they can not only "belong" but also bathe in the reflected glory of the breed as a whole. For most men there probably is just more fun and satisfaction in working with a uniform flock or herd of purebreds than in working with grades or scrubs. As one farmer put it, "The extra five or ten per cent efficiency of a well-planned but heterogeneous group of grade animals is just not sufficient compensation to pay me for what I lose in satisfaction by not having typical representatives of a well-defined, homogeneous group of purebreds."

It may be concluded, therefore, that crossbreeding for purposes of producing superior stock for slaughter is a feasible thing for breeders who can maintain fairly large herds of the purebreds; that the system has possibilities for the creation of new breeds embodying groups of characteristics now found individually in two or more; but that this task should be left in the hands of government or agricultural experiment station experts. Crossbreeding is also an extremely useful tool for the study of the behavior of characteristics in hereditary transmission.

Outcrossing.—The systems of breeding previously discussed in this chapter; *viz.*, hybridization, grading, and crossbreeding involve the mating of unrelated animals that do not belong in any one breed; in other words, they involve the uniting of very diverse bits of germ plasm. Outcrossing, on the other hand, is the mating of animals that are members of the same breed but show no relationship for at least the first four to six generations. As indicated in the early chapters of this book, it seems probable that all organisms extant and extinct which have ever lived on this planet are somewhat related. The theory of evolution suggests that all living things trace back to a single, or perhaps a few, similar origins. Cattle, sheep, and goats belong to the family Bovidae; *i.e.*, they have come through variation from the same progenitors. In the early stages of this diversification, the germ plasms were still compatible and the animals interfertile. Continued variation and selection among the genes finally reached the point where the germ plasm of cattle was not compatible with that of sheep, the animals, therefore, being sterile with each other.

So in the broad view all cattle are related and, of course, still interfertile. All cattle, in other words, probably have many genes in common. But for practical purposes, an animal that shows no common ancestor on both sides of its pedigree for four or five generations is called an *outcross*. To put it another way, when we mate two unrelated animals, their offspring is called an *outcross*. The term *outcrossing* is also used to signify the selection of an unrelated male to use on a group of inbred females with the inference that the breeder will subsequently return to his inbreeding. It is used, in other words, to introduce some desirable genes into an inbred stock.

Most of our purebred animals are the result of outcrossing. The mating of unrelated animals sometimes results very favorably, to be sure, but it is also a fact that most breeders who achieve distinction do so by (1) securing desirable animals of certain strains or families in their particular breed and (2) intensifying the good characteristics of these animals through close- or linebreeding. Nevertheless, the master breeders at times have recourse to outcrossing for its regenerative effect or for the purpose of introducing new genes. Only when used in these latter ways with a specific aim in view is outcrossing to be commended.

Outcrossing is a relatively safe system of breeding to use, for it is unlikely that two unrelated animals in a breed selected more or less at random will both be carrying the same undesirable genes and pass them along to their offspring. Outcrossing is a sort of nothing-venture nothing-gain system. However, the purebred breeder with average or below-average animals is well-advised to use this system, for his problem is to retain a heterozygous type of germ plasm so that the undesirable genes will have as their complement a desirable gene rather than rendering the undesirable ones homozygous as inbreeding is liable to do.

The Committee on Investigations of the American Society of Animal Production with W. V. Lambert as chairman submitted the following report in regard to terminology to describe the progeny from various systems of breeding at the 1940 meeting.

Crossbred. The progeny resulting from the mating of different breeds or, in the case of poultry, different breeds or varieties.

Incross. The progeny resulting from the crossing of individuals of inbred lines within the same breed, or variety.

Inbred Line. The progeny resulting from breeding closely related animals. To be classed as an inbred strain, the individuals should have an average coefficient of inbreeding of 37.5% (equivalent to 2 generations of brother-sister matings).

Incrossbred. The progeny resulting from the crossing of individuals from inbred lines of different breeds, or varieties.

Outcross. A cross of relatively unrelated animals within the same breed, or variety.

Topcross. The mating of a male of a certain family to females of another family of the same breed, or variety.

Topincross. The progeny resulting from the cross of inbred sires on noninbred dams of the same breed, or variety.

Topcrossbred. The progeny resulting from the mating of inbred sires with non-inbred dams of different breeds, or varieties.

Heterosis (or Hybrid Vigor). The superiority over the better parent that is exhibited by the progeny. This applies to the progeny from the crossing of strains, varieties, breeds, or species. The committee suggested that this terminology is sufficiently inclusive to describe various types of crosses without the use of the term "hybrid."[1]

No decision could be reached on the term "hybrid" in view of the many different interpretations of the word.[1]

Summary.—We have discussed in this chapter the various systems of breeding included under the general term of *outbreeding.* Grading up a herd or flock through the use of good purebred sires has long ago proved its worth and will probably continue for some time to be the widest used system of breeding. The various types of crossbreeding also have desirable as well as undesirable points, but like grading their success depends upon the genetic value of the purebreds used. New breeds in any class of stock can be formed through crossbreeding. It would seem, however, that there is enough variety of breeds among all classes of livestock to suit any choice and enough variety in any breed to permit the reaching of any reasonable ideal. If the desired standard in dairy cattle is 15,000 lb. of 4.2 per cent milk, it would seem that this goal could be reached by selection within the present pure breeds more easily than by mixing up several breeds and then attempting to get by selection what is desired. This latter process savors a lot of unscrambling eggs. The disadvantages of crossbreeding in any case must be weighed against its advantages, and its final success or failure depends upon the merit of the purebreds which are used.

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[1] See *Amer. Soc. Anim. Prod. Proc.*, 1940, p. 378; and *Jour. Anim. Sci., February*, 1942, Vol. 1, No. 1, p. 90.

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CHAPTER XXI

SYSTEMS OF BREEDING—RELATED ANIMALS

The last chapter dealt with the systems of breeding involved in the mating of unrelated animals, which were defined as those having no common ancestors on both sides of their pedigrees for at least the first 4 to 6 generations. It would be possible to bring to America 20 sows and 3 or 4 boars of some foreign breed and thus establish the new breed in America. The animals would become scattered to all parts of the country, somewhat different ideals of perfection might be set up in the different sections, and after 30 or 40 generations there perhaps would be several thousands of animals in the breed. Most of the matings would then probably be between boars and sows that had no common ancestors in the first few generations of their pedigrees. Such matings would be called *outcrossing*, although all the animals in this breed would trace back to some of the original 20 sows and 3 or 4 boars and would, therefore, be more or less related. Mutations, different selection ideals, and the sampling nature of the hereditary process would have made some of the sectional strains quite different genetically, although all of the animals in the breed would probably have some genes in common. In fact, all living organisms are related, to some extent, from an evolutionary standpoint, and it is not inconceivable that all may have some genes in common.

Any two cattle of the present day trace back eventually to the few animals that through variation actually gave rise to the class of animals we now know as cattle. So much mutation, variation, selection, and recombination has transpired since that remote time that the fact that all cattle are of the same "blood" means little or nothing so far as their present genetic make-up is concerned.

It would be very interesting if you and I could throw on a moving-picture screen a parade of our ancestors, generation by generation, starting with our two parents, then following with our four grandparents, then our eight great grandparents, etc. Occasionally, if all the facts were known about these people, we might be inclined to blush and would be reminded of a saying attributed to Mark Twain that "man is the only animal that blushes or needs to." If our parade extended back to the time of Christ, there would probably be lots of duplications in it, since this would involve about 69 generations, counting 28 years to a generation, and, since the number of ancestors doubles in each generation, it would mean a total of 2^{69} or about 600,000,000,000,000,000,000 indi-

viduals in the single generation of our pedigree in A.D. 1. It is obvious that this many people were not alive at that time (there are more people in the world now than ever before, about 2 billion) or, in other words, that the same individuals occurred many times in that and other generations of our pedigree. Your pedigree and mine would probably also show many duplications.

In the sense here used, therefore, "related" animals are those with one or more common ancestors within the first 4 to 6 generations and, therefore, with probably more than the average number of genes in common. When two such animals are mated, we call this *inbreeding*. Diverse opinions are held regarding the practice of inbreeding. Speaking generally, it is in bad repute, because it is believed to result in a more or less degenerate offspring. There can be no doubt, however, that many cases of improvement have also resulted from its use.

Inbreeding is commonly divided into two categories, *viz.*, closebreeding and linebreeding. Closebreeding is the mating of a full brother to sister, of sire to his daughter, or dam to her son. These types of matings give the greatest concentration of similar "blood," and this concentration appears close up in pedigree. In fact, the concentration is discovered in the second generation back in all the cases listed as examples of closebreeding. Linebreeding is the mating of animals of wider degrees of relationship than those just stipulated for closebreeding, and is generally directed toward keeping the relationship high to some desirable ancestor or "line" of ancestors. In outline form, this is as follows:

- Inbreeding
  - Closebreeding
    - Sire to daughter
    - Son to dam
    - Full brother and sister
  - Linebreeding
    - Half brother and sister or matings of animals more distantly related; *e.g.*, cousin matings, etc.

Two animals that have any close-up ancestors in common are related, and, if we mate such animals, we are practicing some degree of inbreeding.

Relationships.—There are two ways in which animals may be related, *viz.*, directly and/or collaterally. You are directly related to your father, for you are his offspring, and your pedigrees would show many duplications, as indicated in Fig. 131.

- You
  - A
    - C
    - D
  - B
    - E
    - F
- Your father A
  - C
  - D

FIG. 131.—Schematic pedigrees to show father and son relationship (direct).

Being related to your father means genetically that you and he have more genes in common than do unrelated members of *Homo sapiens*. This is because you both have some common close ancestors. Your father got certain genes from C and D (Fig. 131). You also got some genes from C and D through your father A. One-half of your genes are identical with those your father had, except for a slight discrepancy due to the probable inequality in genes between the X and the Y chromosome if you are a male, and you are therefore related to your father by 50 per cent. Organisms that have common ancestors are related, related organisms probably have more identical genes than nonrelated organisms of the species, and, if related animals are mated, they may both pass duplicate genes to their offspring. In other words, inbreeding has a tendency to make animals more homozygous.

The other type of relationship is called *collateral*. You and your cousin are collateral relatives because you have some ancestors in common. This is illustrated in Fig. 132.

You { *A* Your father { *C* *D* ; *B* }

Your cousin { *Z* Your uncle { *C* *D* ; *Y* }

FIG. 132.—Schematic pedigrees to show cousin relationship (collateral).

You and your cousin probably have some identical genes that came to each of you from your common grandparents, C and D. You got yours through your father, A, your cousin got his through his father, Z (your father's brother or your uncle). The common grandfather, C, might have had a pair of genes *MM* and the common grandmother *mm*. Both your father and your uncle would then have been *Mm*. Whether you and your cousin both got gene *M* or both got gene *m*, or you got *M* and your cousin *m* or vice versa is a matter of chance. With many thousands of genes concerned, however, it is very unlikely that you and your cousin got different members of each pair of heterozygous genes, and these grandparents probably had many homozygous gene pairs in which cases you and your cousin were sure to get identical genes. In other words, it is very likely that you both received some identical genes from your common grandparents.

All cattle probably have some genes in common, but if we mate

Sire X with genes *AA bb Cc Dd Ee FF*

with

Dam Y with genes *AA Bb cc Dd EE ff*

we can have

Kinds of full sisters..................	$1 \times 2 \times 2 \times 3 \times 2 \times 1 = 24$
Kinds of paternal half-sisters..........	$2 \times 2 \times 3 \times 3 \times 3 \times 2 = 144$
Kinds in the breed....................	$3 \times 3 \times 3 \times 3 \times 3 \times 3 = 729$

for the genes, unless closely linked in the same chromosome, can become recombined into all the possible combinations. Genetically, therefore, identity of pedigree, except in the case of identical twins, means only similarity of genes unless the animals have become very homozygous through inbreeding and selection. Most of our animals at present, however, are probably rather heterozygous in their genetic make-up; in other words, they received many different genes from each of their parents, a few similar ones.

The two following animals X and Y are full brothers.

$$X\begin{cases}\text{S }(Aa)\text{ 1 pair of genes}\\ \text{D}\end{cases}\qquad Y\begin{cases}\text{S }(Aa)\\ \text{D}\end{cases}$$

FIG. 133.—Schematic pedigrees of two full brothers.

Animal X might get gene *A* or gene *a* from S, and animal Y might get *A* or *a* from S. Since there is ½ chance that X will get *A* and ½ chance that Y will get *A*, then the chance that both will get *A* is ¼. They might get 100 per cent the same gene (both *A*, ¼ chance, both *a*, ¼ chance); they might get 0 per cent the same gene (one get *A* and the other *a*, ¼ chance or one get *a* and the other *A*, ¼ chance). Therefore, on the average there is a 50 per cent (½) chance that they will both get the same gene from S. Since the same is true as to genes from the dam D, then X and Y have on the average ½ × ½, or ¼, of their genes as duplicates from S and ½ × ½, or ¼, of their genes as duplicates from D, which means that on the average ½ of the genes in X and Y are identical, and they are, therefore, related by 50 per cent, although they have 100 per cent the same "blood." X and Y are full brothers but are only 50 per cent related because of the sampling nature of inheritance, the fact that a parent passes along only a sample half of its total genetic material to any offspring.

The formula for relationship between X and Y is, therefore,

$$R_{xy} = \text{summation of } [(\tfrac{1}{2})^{n+n^1}].$$

The fraction ½ stands for the halving or sampling process of inheritance in each generation, n stands for the number of times this halving or sampling has gone on between S and X, and n^1 stands for the number of times the halving process has gone on between S and Y. Therefore,

for S, $R = \frac{1}{2}^{1+1}$ or $\frac{1}{2}^2$ or 25%
and for D, $R = \frac{1}{2}^{1+1}$ or $\frac{1}{2}^2$ or 25%
and the summation is $R_{xy} =$ 50%

In a similar fashion it can be shown that in half brothers or sisters ¼ of the genes on the average will be identical, and these animals are therefore related by 25 per cent. Similarly, half first cousins as illustrated in Fig. 134 will have 1/16 of their genes identical and will, therefore, be related by 6.25 per cent.

$$A\begin{cases}B\begin{cases}D\\E\end{cases}\\C\begin{cases}F\\G\end{cases}\end{cases}\qquad X\begin{cases}Y\begin{cases}D\\W\end{cases}\\S\begin{cases}M\\N\end{cases}\end{cases}$$

FIG. 134.—Schematic pedigree of half first cousins.

In all cases of relationship, we simply apply the formula R_{xy} = summation of all lines of inheritance reaching the related animals from all the common ancestors that they have $[(\frac{1}{2})^{n+n^1}]$. For the father-son relationship (Fig. 131) we would have $R_{\text{you-your father}} = \frac{1}{2}^{1+0} = \frac{1}{2} = 50\%$, for there is one generation between you and your father, or, in other words, the genetic material has been halved once in getting from your father to you, and there is no generation between your father and himself. Likewise, in Fig. 134, the relationship between A and X is

$$R_{ax} = \frac{1}{2}^{2+2} = \frac{1}{2}^4 = \frac{1}{16} = 6.25\%.$$

The figure 6.25 per cent means that A and X probably have 1/16, or 6.25 per cent, more identical genes than unrelated animals of their species and breed.

In the following two pedigrees of double first cousins we have still 100 per cent the same "blood"; *i.e.*, both A and B get all their "blood" from M and N but the sampling process has gone through one more generation, so that A and B are only 25 per cent related.

$$A\begin{cases}C\begin{cases}M\\N\end{cases}\\D\begin{cases}M\\N\end{cases}\end{cases}\qquad B\begin{cases}E\begin{cases}M\\N\end{cases}\\F\begin{cases}M\\N\end{cases}\end{cases}$$

FIG. 135.—Schematic pedigree showing 25 per cent relationship.

Applying the relationship formula to A and B we have

for M, $R = \frac{1}{2}^{2+2}$ on paternal side + $\frac{1}{2}^{2+2}$ on maternal side = 12.5%
and for N, $R = \frac{1}{2}^{2+2}$ on paternal side + $\frac{1}{2}^{2+2}$ on maternal side = 12.5%
and the summation, R_{AB} = 25%

The term "blood" is being put into quotation marks, because, although it is the usual way the breeder expresses the idea of inheritance, actually, of course, blood does not function in inheritance, this mechanism being provided in the germ cells with their chromosomes and genes. Each embryo produces its own blood, and the only way any animal can get any blood from another, even its own mother, is by means of a blood transfusion. Used in this sense, the term "blood" means inheritance, or chromosomes and genes.

We might of course have both direct and collateral relationship at the same time, as illustrated in Fig. 136.

$$D\begin{cases}E\begin{cases}B\\C\end{cases}\\F\begin{cases}B\\H\end{cases}\end{cases}\qquad E\begin{cases}B\\C\end{cases}$$

FIG. 136.—Simultaneous direct and collateral relationship.

In Fig. 136, D and E are related both directly and collaterally for E is an ancestor (sire) of D (direct), and B is an ancestor of D (through F) and E (collateral). The direct relationship of D and E is expressed by

$$\tfrac{1}{2}^{1+0} = \tfrac{1}{2} = 50\%$$

and the collateral relationship by

$$\tfrac{1}{2}^{2+1} = \tfrac{1}{2}^{3} = \underline{12.5\%}$$

Summating, we have

$$R_{DE} = 62.5\%$$

That is, since E is the sire of D, then D got half of his genes from E and is related to E by 50 per cent. In addition, D and E are related through B, which is the sire of E and also the maternal grandsire of D. What we are asking is how many of the genes that E has are also likely to be found in D, and the answer is 62.5%. If an animal that is a common ancestor of two related animals is itself inbred and, therefore, more homozygous, a correction for this fact must be made in the formula for relationship; and likewise, if the animal itself is more inbred than the ancestor, a correction must be made. These corrections will be indicated after we have discussed the coefficient of inbreeding.

Figure 137 shows the pedigree of the Holstein bull N.J.E.S. Mutual Ormsby Jewel Alice. This bull carries 62.5 per cent of the "blood" of Ormsby Sensation 45th getting 25 per cent from each of the latter bull's appearances in the second generation of the pedigree and 12.5 per cent from his appearance in the third generation. Since the amount of Ormsby Sensation 45th "blood" in the bull N.J.E.S. Mutual Ormsby Jewel Alice is the average of that found in his parents, we could find the

amount in N.J.E.S. Mutual Ormsby Jewel Alice by averaging the amounts in Newmont Mutual Ormsby Lad and Newmont Ormsby Jewel Alice. The former has 50 per cent of Ormsby Sensation 45th "blood" and the latter 75 per cent, the average of the total of the two parents being 62.5 per cent as noted above. N.J.E.S. Mutual Ormsby Jewel Alice is 62.5 per cent, Newmont Mutual Ormsby Lad 50 per cent, and Newmont Ormsby Jewel Alice 75 per cent related to Ormsby Sensation 45th.

Name, N.J.E.S. Mutual Ormsby Jewel Alice No. 654594 Born Dec. 1, 1931	Newmont Mutual Ormsby Lad, 493889	Ormsby Sensation 45th, 442551	Ormsby Sensation, 274343
			Shady Maple King Pontiac Hockster, 219580
		Newmont Mutual Scotia, 575310	Sir Mutual Scotia, 170631
			Isa Scotia Beets, 315248
	Newmont Ormsby Jewel Alice, 1239022	Ormsby Sensation 45th, 442551	Ormsby Sensation, 274343
			Shady Maple King Pontiac Hockster, 219580
		Newmont Ormsby Jewel, 1094461	Ormsby Sensation 45th, 442551
			Clothilde Maid Ormsby Bess

FIG. 137.—Holstein pedigree showing collateral relationship.

Since the sire and dam of N.J.E.S. Mutual Ormsby Jewel Alice are collaterally related, *i.e.*, have one or more common ancestors, this bull is inbred. He is likely to have gotten identical genes from Ormsby Sensation 45th through three different lines, *viz.*, through his sire, his dam, and his maternal granddam. To find the relationship between the sire and dam, we must trace all these lines and count the generations involved according to our formula $R_{xy} = \Sigma^*[(\frac{1}{2})^{n+n'}]$.

From sire to Ormsby Sensation 45th = 1
From dam to Ormsby Sensation 45th = 1 $\quad \therefore \frac{1}{2}^{1+1} = \frac{1}{2}^{2} = 25.0\%$
From sire to Ormsby Sensation 45th = 1
From dam through maternal granddam
to Ormsby Sensation 45th = 2 $\quad \therefore \frac{1}{2}^{1+2} = \frac{1}{2}^{3} = 12.5\%$

37.5%

That is, Newmont Mutual Ormsby Lad and Newmont Ormsby Jewel Alice are 37.5 per cent related (small correction needed for inbreeding involved).

* **Greek letter sigma is used for summation.**

A simpler way of finding this relationship, since these animals are collaterally related through only one common ancestor (Ormsby Sensation 45th), would have been to multiply the percentage of Ormsby Sensation 45th "blood" in each (50 × 75 = 37.5). This latter method becomes complicated, however, where there is more than one common ancestor, especially if these are related.

It may help to simplify matters by writing the pedigree of N.J.E.S. Mutual Ormsby Jewel Alice in a little different form and using letters of the alphabet instead of the actual names. This is done in Fig. 138.

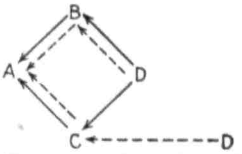


FIG. 138.—Simplified pedigree of Fig. 137.

The solid lines from D (Ormsby Sensation 45th) to B and C indicate that both B and C are by D, and that some identical genes may have reached A from D through these two different paths. The same possibility holds for some other identical genes reaching A from D through the paths indicated by the broken lines.

Direct relationship is what most breeders refer to as *percentage of blood.* They say an animal gets 50 per cent of its "blood" from its sire, 50 per cent from its dam, 25 per cent from each grandparent, 12.5 per cent from each great grandparent, etc., as illustrated in Fig. 139, together with the figures of chromosomes below using cattle with 60 chromosomes as the example.

Animal A 100% (60)	Sire 50% (30)	Grandsire 25% (15)	Great grandsire 12.5% (7 or 8)	Great great grandsire 6.25% (3 or 4)
			Great granddam	
		Granddam 25% (15)		
	Dam 50% (30)	Grandsire 25% (15)		
		Granddam 25% (15)		
Total blood each generation	100%	100%	100%	100%
Total chromosomes each generation	(60)	(60)	(60)	(60)

FIG. 139.—Showing most probable distribution of "blood" and chromosomes in a cattle pedigree.

Each parent in Fig. 139, is shown as having contributed 30 chromosomes to animal A. These 30 chromosomes were a random sample

half of the 60 chromosomes that each of these parents had. The figure shows 15 of them to have come from each grandsire and granddam. This may or may not have been true in any individual case. It would be possible for the 30 chromosomes that the sire passed on to animal A to have all come from the sire's sire (or from the sire's dam), thus in genetic terms actually terminating one line of the pedigree at that point. It will be noted that there are 60 chromosomes in each generation of the pedigree. In animal A they are found in their entirety. In the parental generation, they are divided between two individuals, the sire and dam. In the grandparental generation, they are divided among four individuals, etc. This illustrates why it is generally not important

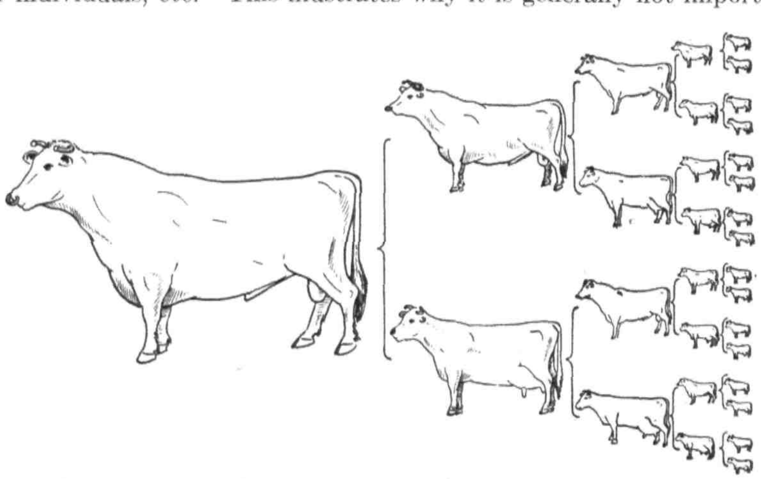


FIG. 140.—Pictorial pedigree showing relative size of ancestors in terms of their contribution according to Galton's law.

to trace or consider pedigrees for more than three or four generations, and also why it is unnecessary to pay any particular attention to an outstandingly good or poor individual that occurs farther back than the fourth or fifth generation.

As far as direct relationships are concerned, "percentage of blood" and degree of relationship are seen to be the same thing. It is a mistake, however, to try to use "percentage of common blood" as a measure of relationship between animals related collaterally. Figure 133 showed two full brothers X and Y to have 100 per cent the same "blood" and to be related by 50 per cent. Figure 135 on the other hand showed the two double first cousins A and B also to have 100 per cent the same "blood" but to be related by only 25 per cent because of the additional intervening generation.

Coefficient of Inbreeding.—As indicated earlier, inbreeding results whenever related animals are mated. We have already seen that

full brothers and sisters are related by 50 per cent; *i.e.*, ½ of their genes are probably identical (¼ from each parent). Now, if a full brother and sister are mated, we produce a new generation that is once further removed from the common ancestors. Since each such removal halves the genetic material, we can simply divide the relationships between the full brother and sister (50 per cent) by ½ and thus arrive at the coefficient of inbreeding for the new individual. Figure 141 represents such a mating.

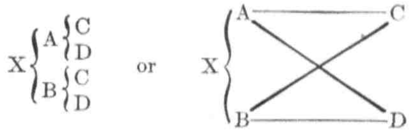


FIG. 141.—Full brother-sister mating.

In other words, to find the coefficient of inbreeding of any animal we can first find the coefficient of relationship between its sire and dam and then divide this amount by 2.

Another way to do this is to count the number of times the genetic material has been halved in getting to the parents of the inbred animal from the common ancestor (or ancestors) and then adding 1 to the exponent of ½ to take care of the halving in getting from the sire and dam to the inbred animal in question. This gives us the formula for inbreeding suggested by Wright[1] as

$$F_x = \Sigma[(\tfrac{1}{2})^{n+n^1+1}]^*$$

This formula measures the reduction of heterozygosity in relation to the foundation stock in the most remote generation of the pedigree being considered. Figure 142 shows a half brother-sister mating, B and C being 25 per cent related, because there is one generation from B back to the common ancestor D and also one generation from C back to D.

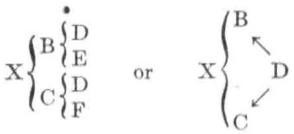


FIG. 142.—Schematic half brother-sister mating.

The only common ancestor here is D. From the sire back to the common ancestor is 1 (n in formula); from the dam back to the common ancestor is 1 (n^1 in formula); and the 1 that must be added to take care of the halving in getting from B and C to X gives us a total of 3 as the

[1] WRIGHT, S., Coefficients of Inbreeding, *Amer. Nat.*, **56**: 330–338, 1922.

* Complete formula will be found below.

exponent of $\frac{1}{2}$, and $\frac{1}{2}^3 = \frac{1}{8}$, or 12.5 per cent as the inbreeding coefficient of X. This figure 12.5 per cent simply means that this system of mating has reduced the heterozygosity (or increased the homozygosity) by that amount over what it was in the generation containing D, E, and F. If the animals D, E, and F were 50 per cent homozygous and 50 per cent heterozygous, then animal X is 12.5 per cent less heterozygous or $50\% \times 12.5\% = 6.25\%$ less heterozygous than they were, or only 43.75 per cent heterozygous. Looked at the other way, X is now 56.25 per cent homozygous.

If a common ancestor is himself or herself inbred, this will, of course, make a difference in the likelihood of its inbred descendant getting identical genes from each of its parents. Being inbred means that the common ancestor (A) is homozygous for more pairs of genes than is an outbred one. In other words, two offspring of such an inbred animal have less chance of receiving different genes from this ancestor and likewise more chance of receiving identical genes. This fact is provided for by changing our formula for inbreeding from

$$F_x = \Sigma[(\tfrac{1}{2})^{n+n+1}] \qquad \text{to} \qquad F_x = \Sigma[(\tfrac{1}{2})^{n+n'+1} \cdot (1 + F_A)]$$

In other words if $\Sigma[(\frac{1}{2})^{n+n'+1}]$ was found in a given case to be 25 per cent, but the common ancestor was himself or herself inbred by 12.5 per cent, then we would have to multiply 25 per cent by 1.125 per cent, making the final inbreeding 28.125 per cent.

A case of this sort is shown in Fig. 143.

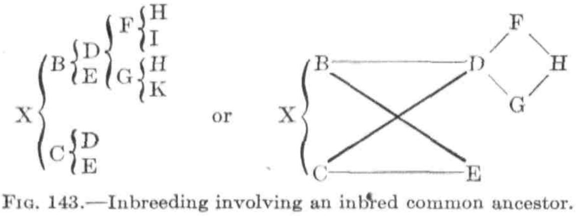


FIG. 143.—Inbreeding involving an inbred common ancestor.

It is obvious in Fig. 143 that X is an inbred animal, for it resulted from the mating of full brother and sister B and C. In other words, X is more homozygous because it received some identical genes from D through its sire and dam and also some from E through its sire and dam. But D, one of the common ancestors, is also seen to have been an inbred animal; in other words, D had more homozygous sets of genes than an outbred animal because he received some identical genes from H through both his sire and his dam. This being the case, D would be expected to have fewer sets of heterozygous genes, one member of which would be passed to X through its sire B and the other member of which would be passed to X through its dam C. If D were not inbred, he might be

homozygous for certain genes, but, if he is inbred, he is undoubtedly homozygous for more sets of genes. Since the coefficient of inbreeding measures directly the probable increase in homozygosity, the inbreeding of any animal must be multiplied by 1 plus the percentage inbreeding of any common ancestors that are themselves inbred, in other words, must be increased by the added amount of homozygosity due to the increased homozygosity of its inbred common ancestors. We cannot, of course, know the actual amount of homo- or heterozygosity for any animal. The coefficient of inbreeding simply accounts for the *added* homozygosity due to the opportunity an animal has of getting identical genes from any ancestors that are common to its sire and dam.

Figure 144 shows the pedigree of an animal that has some repeats in its pedigree but is not an inbred animal because it has no common ancestor on both sides of its pedigree; in other words, its sire and dam are not related.

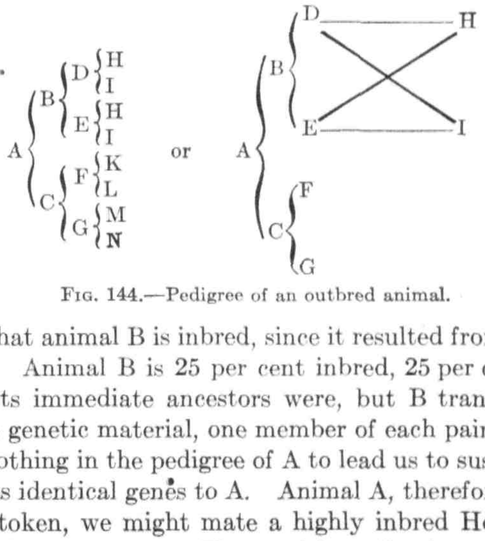


FIG. 144.—Pedigree of an outbred animal.

It is true that animal B is inbred, since it resulted from a full brother-sister mating. Animal B is 25 per cent inbred, 25 per cent more homozygous than its immediate ancestors were, but B transmits to A only one-half of its genetic material, one member of each pair of genes that it has, there is nothing in the pedigree of A to lead us to suspect that B and and C will pass identical genes to A. Animal A, therefore, is not inbred. By the same token, we might mate a highly inbred Holstein bull to a highly inbred Guernsey cow. The resulting offspring would, of course, not be inbred, although both of its parents were, but crossbred. The inbred Holstein and Guernsey would not be likely to pass identical genes to their offspring, although since they both belong to the species cattle, they probably do have some genes in common and might, therefore, pass some identical genes to their offspring.

A decline in heterozygosity should result automatically under continued self-fertilization or closebreeding. Thus an individual heterozygous for a single factor pair *Aa* will produce, if selfed, offspring of which one-fourth are *AA*, one-half *Aa*, and one-fourth *aa*. Under continued selfing the homozygous types

breed true and are progressively augmented by segregates from the dwindling group of heterozygotes. The proportions of the three groups may be determined for any generation by the formula developed by Mendel:

$$2^n - 1\ AA : 2\ Aa : 2^n - 1\ aa$$

where n is the number of generations of self-fertilization.

Similar formulas have been developed by which it is possible to compute the results of other systems of mating. Thus in brother-sister mating the proportion of homozygosity progressively increases but at a slower rate, 6 generations of self-fertilization being approximately as effective as 17 generations of brother-sister mating.[1]

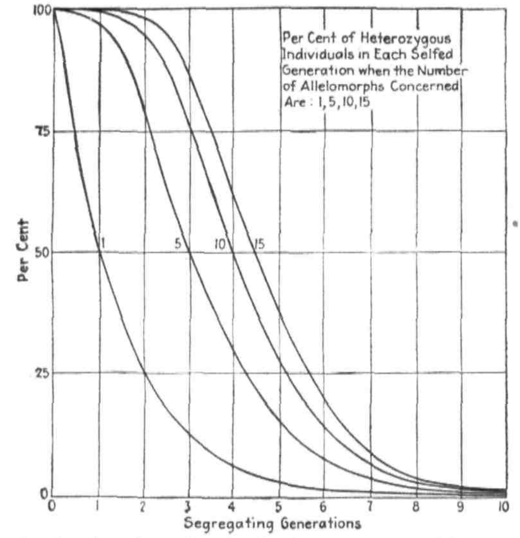


FIG. 145.—Graphs showing the reduction in the proportion of heterozygous individuals and of heterozygous factor pairs in successive generations of self-fertilization. (*After East and Jones.*)

This reduction in heterozygosity takes place automatically in all other factor pairs regardless of the number of pairs involved (Fig. 145). Thus continued self-fertilization leads to a decline in heterozygosity for about seven generations, about 99 per cent of homozygosity being attained in the seventh generation. This resembles the actual results of inbreeding, for here there is a decline in size and variability for about seven or eight generations, after which a line becomes essentially stable.

All the evidence can best be interpreted, therefore, as indicating that the reduction in size and vigor is related in some way to the attainment of homozygosity and that the mere process of inbreeding, *of itself*, does not produce this result. The automatic reduction of heterozygosity will occur, of course, only if

[1] From EAST, E. M., and JONES, D. F., "Inbreeding and Outbreeding," J. B. Lippincott Company, Philadelphia, 1919.

new mutations in inbred lines are very rare. If the mutation rate is high, this may defer or prevent the attainment of homozygosity.[1]

Coefficient of Relationship.—Because of the fact that inbreeding makes an animal more homozygous, and, therefore, if a common ancestor of two related animals makes it more likely that he will pass identical genes to both descendants, and also because inbreeding makes a population more variable by producing separate inbred strains, two corrections are needed in the formula for relationship to make it scientifically correct. To take care of the fact that an inbred common ancestor is more likely to pass identical genes to two descendants, because his inbreeding has made him more homozygous, the numerator of the relationship coefficient must have added to it $(1 + F_a)$ as a multiplier, as we have just seen, and to take care of the fact that inbreeding tends to create separate families a denominator must be supplied in the form of $1 + F_x$, $1 + F_y$ making the complete formula for relationship between animals X and Y.

$$R_{xy} = \frac{\Sigma[(\frac{1}{2})^{n+n^1} \cdot (1 + F_a)]}{\sqrt{1 + F_x} \cdot \sqrt{1 + F_y}}$$

In a parent-offspring relationship with the parents not inbred, the result is $\frac{75\%}{\sqrt{1 + F_0}}$. In the mating, for instance, of a son to his own dam the most probable situation is that in half the pairs of genes in the offspring both members will have come from the common ancestor. But in half those cases the two genes will be duplicates of only one gene that the common ancestor had, so that in one-quarter of the pairs of genes the offspring will be homozygous, whereas the common ancestor was heterozygous, although both of the offsprings' genes came from the common ancestor. This is illustrated in Fig. 146.

$$O \begin{cases} S \begin{cases} F \\ D \end{cases} \\ D \end{cases} \qquad F_{OD} = \frac{75}{\sqrt{1 + F_0}} = \frac{75}{\sqrt{1 + 0.25}} = \frac{75}{1.1} = 68.2$$

FIG. 146.—Parent-offspring mating with relationship computed.

The real function of these corrections is to reveal the actual degree in which the genotype of related animals are similar, rather than leave it in terms of the percentage of genes from a common source. In the above parent-offspring mating, it is most likely that 75 per cent of the genes of the offspring O came from its dam and paternal granddam D, but, since the offspring is inbred, whereas the parent D was not, then O will have a certain number of homozygous gene pairs that existed as heterozygous pairs in the parent D.

[1] SINNOTT, E. W., and DUNN, L. C., "Principles of Genetics," McGraw-Hill Book Company, Inc., New York, 1939.

Because there has been so little inbreeding practiced in our farm livestock, the denominator of the complete relationship coefficient seldom becomes very much larger than 1.0 and can, therefore, be dispensed with in general practice.

The final form of the formula for direct or ancestor-descendant relationship becomes

$$R_{xa} = \Sigma \left(\frac{1}{2}^{n}\right) \sqrt{\frac{1 + F_a}{1 + F_x}}$$

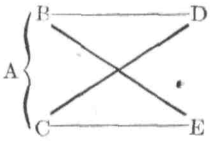
The term under the square-root sign in this formula is necessary owing to the fact that, if the ancestor is more highly inbred (more homozygous) than the descendant, the coefficient of relationship will be larger than the "percentage of blood," and vice versa. In most pedigrees of our farm animals, however, there is not likely to be enough difference in the amount of inbreeding of ancestor and descendant but that the portion of the complete formula under the radical can be dispensed with.

The following table will be found convenient in working out inbreeding coefficients.

TABLE 41.—EXPONENTIAL VALUES OF ½

$\frac{1}{2}^2$ = ¼	=	25.0%
$\frac{1}{2}^3$ = ⅛	=	12.5%
$\frac{1}{2}^4$ = 1/16	=	6.25%
$\frac{1}{2}^5$ = 1/32	=	3.125%
$\frac{1}{2}^6$ = 1/64	=	1.5625%
$\frac{1}{2}^7$ = 1/128	=	0.78125%
$\frac{1}{2}^8$ = 1/256	=	0.390625%
$\frac{1}{2}^9$ = 1/512	=	0.1953125%

In the mating of full brother and sister we have seen that the coefficient of inbreeding is 25 per cent.



In the case of continued full brother-sister matings for two generations the inbreeding coefficient would be 37.5 per cent.

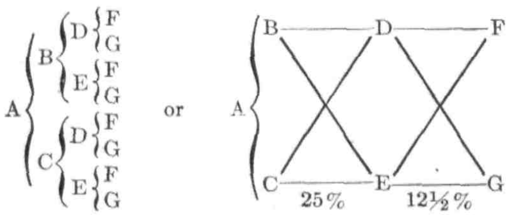


FIG. 147.—Brother-sister matings for two generations.

It should be observed that we trace back from B, the sire, to D, a common ancestor, then down to D on the dam's side of the pedigree, and then forward to the dam. We do this also for E, another common ancestor in the second generation, and this completes all the ancestors in this generation. Now we move to the third generation where we find the same two animals F and G in each line of the pedigree. When we traced the paths through D a moment ago, we also took care of the F's and G's in these lines, since the likelihood of animal A getting identical genes from D is taken care of in its entirety when we trace the D paths and is not increased because of the F's and G's behind D. The same thing applies to the E's in the second generation. However, since the presence of F and G behind D on the top side of the pedigree and behind E on the bottom side (and E on the top side and D on the bottom side) does give additional opportunities for A to get identical genes through these paths, these opportunities must be evaluated.

We have, therefore, in this two-generation full brother-sister mating, four common ancestors, D, E, F, and G, and they have the following values.

$$\begin{aligned}
D &= \tfrac{1}{2}^{1+1+1} &&= \tfrac{1}{2}^{3} &&= 12.5\% \\
E &= \tfrac{1}{2}^{1+1+1} &&= \tfrac{1}{2}^{3} &&= 12.5\% \\
F &= \tfrac{1}{2}^{2+2+1} \times 2 &&= \tfrac{1}{2}^{5} \times 2 &&= 6.25\% \\
G &= \tfrac{1}{2}^{2+2+1} \times 2 &&= \tfrac{1}{2}^{5} \times 2 &&= 6.25\% \\
& && \text{Total} && \quad 37.5\%
\end{aligned}$$

With three generations of full brother-sister matings, we would have

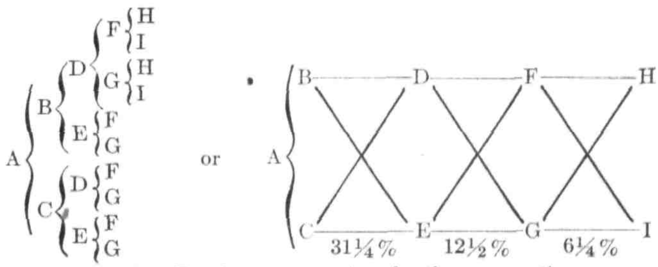


FIG. 148.—Brother-sister matings for three generations.

Here we meet the fact that some of the common ancestors (D and E) are themselves inbred, so that our summation of all the different paths, by means of which A might get identical genes from its common ancestors, is

$$
\begin{aligned}
D &= \tfrac{1}{2^3} \times 12.5 \times 1.25 = 15.625\% \\
E &= \tfrac{1}{2^3} \times 12.5 \times 1.25 = 15.625\% \\
F &= \tfrac{1}{2^5} \times 2 = 6.250\% \\
G &= \tfrac{1}{2^5} \times 2 = 6.250\% \\
H &= \tfrac{1}{2^7} \times 4 = 3.125\% \\
I &= \tfrac{1}{2^7} \times 4 = 3.125\% \\
&\text{Total} \quad 50.000\%
\end{aligned}
$$

In Fig. 148, it is evident that the sire B and dam C are connected through two lines involving two generations, through four lines involving four generations, and through eight lines involving six generations. In

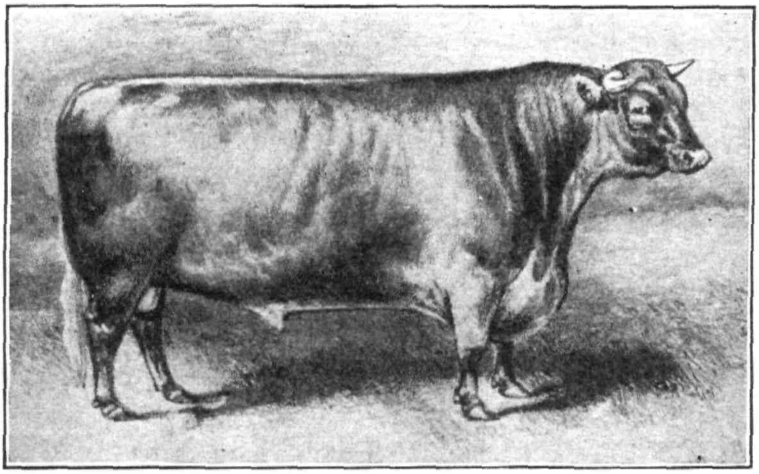


FIG. 149.—Comet (155). The first bull ever sold for $5,000. He was very strongly inbred. (*From Sanders, Shorthorn Cattle, The Breeders Gazette.*)

addition, the parents of the sire and dam have one generation of inbreeding behind them, or 25 per cent. Our formula becomes, therefore,

$$F_x = \Sigma 2[(\tfrac{1}{2})^3 \times 1.25] + 4[(\tfrac{1}{2})^5] + 8[(\tfrac{1}{2})^7] = 50\%$$

This shows that, assuming a 50 per cent heterozygous condition to start with, an individual which is the result of four generations of full brother-sister matings is now 75 per cent homozygous.

In full brother-sister matings one generation gives an inbreeding coefficient of 25 per cent; two generations 37.5 per cent; three generations 50 per cent; ten generations 88.6 per cent. In parent-offspring matings, one generation gives an inbreeding coefficient of 25 per cent; two generations 37.5 per cent; three generations 43.8 per cent, approaching 50 per cent as a limit.

Examples of Inbreeding.—Figure 150 gives the pedigree of the famous Shorthorn bull Comet, the first bull ever sold for as much as $5,000.

Comet (155)
- Favorite (252)
  - Bolingbroke (86)
    - Foljambe (263)
      - R. Barker's bull (52)
      - Haughton
    - Young Strawberry
      - Dalton Duke (188)
      - Favorite (cow)
  - Phoenix
    - Foljambe (263)
      - R. Barker's (bull (52)
      - Haughton
    - Favorite (cow)
      - Alcock's bull (19)
      - ....
- Young Phoenix
  - Favorite (252)
    - Bolingbroke (86)
      - Foljambe (263)
      - Young Strawberry
    - Phoenix
      - Foljambe (263)
      - Favorite (cow)
  - Phoenix
    - Foljambe (263)
      - R. Barker's bull (52)
      - Haughton
    - Favorite (cow)
      - Alcock's bull (19)
      - ....

Fig. 150.—Pedigree of Shorthorn bull, Comet.

As will be noted, the bull Favorite was bred back to his own dam Phoenix and their offspring Young Phoenix bred to her sire Favorite. Since Favorite is himself inbred, we shall first compute his coefficient of inbreeding. His sire and dam are related through the bull Foljambe and the cow Favorite, our formula being

$$F_A = \Sigma[(1/2)^3] + [(1/2)^4] = 18.75\%$$

As shown in the pedigree, Comet has four common ancestors, *viz.*, Favorite (bull), Phoenix, Foljambe, and Favorite (cow), and our formula becomes

$$\begin{aligned} F_x &= \Sigma[(1/2)^2 \times 1.1875] + [(1/2)^3] + [(1/2)^5] + [(1/2)^6] \\ &= 0.2969 + 0.1250 + 0.0312 + 0.0156 \\ &= 46.87\% \text{ coefficient of inbreeding for Comet} \end{aligned}$$

We can perhaps see this more clearly if we skeletonize the pedigree of Comet and use letters instead of names as follows:

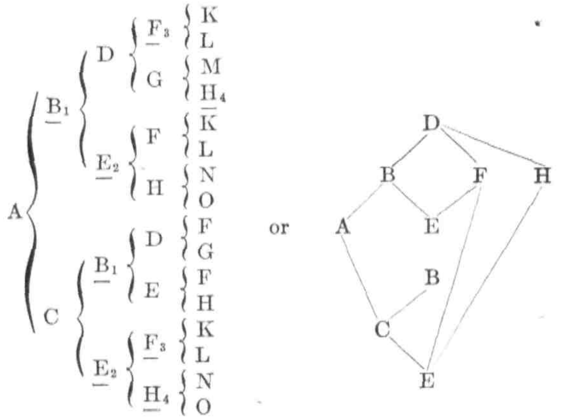


FIG. 151.—Skeletonized pedigree of Comet.

It is evident from Fig. 151 that one of the common ancestors, B, is himself inbred and that E, F, and H are also common ancestors.

Figure 152 gives the pedigree of the Jersey bull Sybil's Gamboge. The sire and dam of this bull are more than half brother and sister, the sire is the result of mating a three-quarter brother and sister, and the dam of Sybil's Gamboge traces in all four lines to the bull Champion Flying Fox, for he is the sire of both Gedney Farm Oxford Lad and of Agatha's Flying Fox.

We notice that there are five ancestors in this pedigree that are common to both sire and dam, *viz.*, Oxford Majesty, Royal Majesty, Gedney Farm Oxford Lad, Fontaine's Oxford Pride, and Champion Flying Fox,

Name: Sybil's Gamboge Registry No.: 174663 Date of Birth: March 16, 1914	Sire: Imp. Gamboge's Royal Majesty 149864	Imp. Oxford Majesty 134090	Royal Majesty 79313	Gedney Farm Oxford Lad 71238
				Oxford Ixia 3rd 8584
			Oxford Lad's Lucy 213913	Gedney Farm Oxford Lad 71238
				Lucy 12th 9236
		Majesty's Pride 2nd 14462	Royal Majesty 79313	Gedney Farm Oxford Lad 71238
				Oxford Ixia 3rd 8584
			Oxford's Fontaine 224580	Gedney Farm Oxford Lad 71238
				Fontaine Oxford Pride 187430
	Dam: Gamboge Oxford Sybil 337787	Imp. Oxford Majesty 134090	Royal Majesty 79313	Gedney Farm Oxford Lad 71238
				Oxford Ixia 3rd 8584
			Oxford Lad's Lucy 213913	Gedney Farm Oxford Lad 71238
				Lucy 12th 9236
		Gamboge's Prosperity 252142	Gamboge's Knight 95698	Agatha's Flying Fox 3256
				Fontaine's Oxford Pride 187430
			Oxford's Fawn Lucy 238439	Gedney Farm Oxford Lad 71238
				Cynthia 7927

FIG. 152.—Pedigree of Sybil's Gamboge.

and we also notice that Oxford Majesty, one of the common ancestors, is himself inbred. We have, therefore,

Oxford Majesty. One chain of two generations, together with his own inbreeding coefficient of 12.5 per cent. Contribution $(\frac{1}{2})^3 \times 1.125$.

Royal Majesty. One chain of four generations (the other chain having been accounted for in working with Oxford Majesty). Contribution $(\frac{1}{2})^5$.

Gedney Farm Oxford Lad. Seven remaining chains of six generations. Contribution $7 \times (\frac{1}{2})^7$.

Fontaine's Oxford Pride. One chain of six generations. Contribution $(\frac{1}{2})^7$.

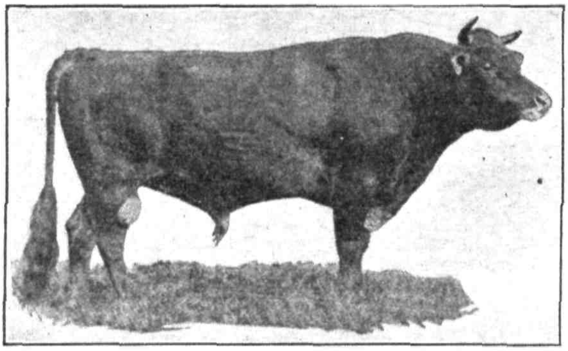


FIG. 153.—Sybil's Gamboge, a strongly inbred Jersey bull.

Champion Flying Fox. Four remaining chains of eight generations. Contribution $4 \times (\frac{1}{2})^9$.

Total. F_x for Sybil's Gamboge = 24.22%.

Role of Inbreeding.—Now that we understand the basic principles underlying inbreeding, it will no longer surprise us that both good and harmful results arise from its use. Inbreeding in itself does not create any new genes, nor for that matter does any system of breeding. All that any system can do is to recombine the genes already present into new combinations. With outbreeding, we tend to keep our livestock heterozygous. With inbreeding, we make them more homozygous. If we have a preponderance of good genes and gene combinations in our stock to start with, inbreeding plus selection will increase the good qualities we already have. If we have a preponderance of poor genes and gene combinations to start with, inbreeding will increase the poor qualities we already have.

What inbreeding actually does is to fix characters. These characters may be either good, bad, or indifferent, and, whatever they are, inbreeding will not change them in the least. Inbreeding is no more potent than

any other system in creating new characters of any sort; in fact, it is less so, for variation is reduced. All that inbreeding does is to take the genes that are present and sort them out into homozygous forms. For instance, if an animal was carrying several genes, or determiners, for characters in the heterozygous form, *i.e.*, one parent after reduction had put in *AbC* and the other one *aBc*, the hybrid would carry *Aa Bb Cc*. If such an animal were bred to another animal of similar genetic constitution, the genes would tend to combine in all possible combinations from *AA BB CC* to *aa bb cc*. Then, if sufficient numbers were available, so that rigid selection could be practiced, the *AA BB CC* type could be selected out. Supposing that in the foregoing, the capital letters stood for desirable characteristics and the small letters for undesirable ones, one can see why inbreeding may give either good or bad results. For *AA BB CC* animals with no recessive, undesirable factors would be a decided improvement over either parent, whereas *aa bb cc* animals would be just the reverse. It will bear repeating that inbreeding is powerless to create either good or bad. It is, however, the very best method of finding out what is present in a strain, for inbreeding will sort out the various genes into a homozygous condition. The desirable animals may then be retained and the undesirable ones discarded.

If a breeder thinks that he has a particularly good sire and really wants to learn the truth, he can do so by mating this sire to 20 of his own daughters, as suggested by Wriedt. Comparisons between the immediate daughters of this sire and the offspring resulting from breeding this sire to his own daughters will provide the answer to the sire's real worth as a breeding male, for it will reveal his genetic make-up by allowing both his dominant and recessive genes to appear in homozygous form.

Bakewell's Work.—Robert Bakewell, an Englishman, born in 1725, was the first man as far as is known who dared to use inbreeding in a constructive way. He worked with Longhorn cattle, Leicester sheep, and Shire horses. It is said that he secured two heifers and a bull after a great search for just what he wanted, and that his entire herd of cattle was developed from these without any outside blood. His success as a breeder was noteworthy, and is today well-known. Culley, writing in 1794, said:

> The great obstacle to the improvement of domestic animals seems to have arisen from a common and prevailing idea amongst breeders that no bull should be used in the same stock more than three years, and no tup more than two; because (say they) if used longer, the breed will be too near akin, and liable to disorders; some have imbibed the prejudice so far as to think it irreligious, and if they were by chance in possession of the best beast on the island would by no means put a male and female together that had the same sire, or were out of the same dam. Mr. Bakewell has not had a cross for upward of 20 years, his best stock has been

bred by the nearest affinities, yet they have not decreased in size, neither are they less hardy, or more liable to disorder, but, on the contrary, have kept in a progressive state of improvement.

Since Bakewell's time, his example has been emulated by many breeders. Breeds are best known by means of individuals and families, and most of the latter have arisen as the result of intensifying the characteristics of certain individuals through inbreeding.

Good Results from Inbreeding.—In practically any breed of livestock it is possible to find animals that have resulted from rather intensive inbreeding. As an example, there is shown on page 503 the pedigree of Sybil's Gamboge, a famous Jersey bull.

It will be agreed that this is a rather closely inbred bull. The bull is a double grandson of Imperial Oxford Majesty, a triple great grandson of Royal Majesty, and a septuple great, great grandson of Gedney Farm Oxford Lad, as well as a triple great, great grandson of Oxford Ixia 3d, a double great, great grandson of Lucy 12th, and a double great, great grandson of Fontaine's Oxford Pride. Royal Majesty founded the Majesty family of Jerseys, which contains many notable show winners and producers. "Get" of Sybil's Gamboge won 14 ribbons at the 1920 National Dairy Show, including one junior champion, three firsts, three seconds, two thirds, two fourths, two fifths, and one sixth, as well as second and fourth in the get of sire.

Sybil's Gamboge has 88 Reg. of Merit daughters whose records on a mature basis average 12,234 lb. of milk testing 5.12 per cent. The best record to be found among these daughters is one of 19,239 lb. of milk and 933 lb. of fat made by Sybil's Miss May as a junior six-year-old cow. Sybil's Gamboge also has 21 proved sons.

The late N. H. Gentry, a successful breeder of Berkshire swine, is quoted by Mumford as having said:

> If it is true that inbreeding intensifies weakness of constitution, lack of vigor, or too great fineness of bone, as we all believe, is it not as reasonable and as certain that you can intensify strength of constitution, heavy bones, or vigor, if you have these traits well developed in the blood of the animals you are inbreeding? I think I have continued to improve my herd, being now able to produce a larger percentage of really superior animals than at any time in the past.

The foregoing examples illustrate the fact that not only during the foundation period of the breeds was inbreeding a potent factor for improvement but that it still retains its potency.

Harm from Inbreeding.—In exactly similar manner, one might unearth opinions and examples both in the past and in the present that would indicate that inbreeding is an extremely dangerous practice and that anyone using it is liable to encounter serious difficulties. This will

not be done, however, for there are many references in the literature of animal husbandry as to the harmful results from the practice of inbreeding.

Experimental Data.—Much experimental work has been done with a view to illuminating the problem of inbreeding. Castle says in regard to some inbreeding experiments with Drosophila:

My pupils and I bred brother and sister for fifty-nine generations in succession without obtaining a diminution in either the vigor or the fecundity of the race, which could with certainty be attributed to that cause. A slight diminution was observed in some cases, but this was wholly obviated when parents were chosen from the more vigorous broods in each generation. Nevertheless, the crossing of two inbred strains of Drosophila, both of which were doing well under inbreeding, produced offspring superior in productiveness to either inbred strain. Even in this case, therefore, though inbreeding is tolerated, crossbreeding has advantages.[1]

Bos and Weismann inbred rats for about thirty generations and secured a diminution in both fertility and vigor (see Chap. X). King also inbred rats for 25 generations and, according to Hays, found that:

Inbred males in seventh to fifteenth generations were 18 per cent heavier than check males not inbred. Inbred females were about 3.7 per cent heavier than controls at one year old. The variability in body weight at maturity of the fifteenth generation of inbred males and females was about 40 per cent less than among the control animals. King (1918) also studied the effect of inbreeding on fertility, the time of puberty, and the longevity of albino rats inbred by brother and sister mating for twenty-five generations. The average size of litter of all inbred matings was 7.5 rats; and the average litter size for controls 6.7 rats. Inbred rats seemed to reach sexual maturity and to breed slightly earlier than stock females not inbred . . . The number of sterile animals is not given, but King states that inbreeding did not decrease the productiveness of the animals. Inbred rats lived longer than control animals not inbred. The value of selection in inbreeding animals is concisely illustrated in this painstaking and thorough study of the question of inbreeding.[2]

Reporting on his extensive investigations, Wright says:

There has been an average decline in vigor in all characteristics during the course of 13 years of inbreeding of guinea pigs, brother with sister. The decline is most marked in the frequency and size of litter, in which it is so great that it would have to be accounted for even though the decline in other respects was assumed to be due wholly to a deterioration in the environmental conditions. The decline is greater in the gains after birth than in the birth weight, and greater in the percentage raised of the young born alive than in the percentage born alive. The ability to raise larger litters has fallen off much more than ability to raise small litters.

[1] Castle, W. E., "Genetics and Eugenics," p. 221, Harvard University Press, Cambridge, Mass., 1916.

[2] Hays, F. A., Inbreeding Animals, *Del. Agr. Expt. Sta. Bul.* 123, p. 15, 1919.

A comparison of the inbred guinea pigs with a control stock, raised under identical conditions without inbreeding, and derived in the main from the same linebred stock as the inbred families, indicates that the inbreds have suffered a genetic decline in vigor in all characteristics. The decline in fertility is again shown to be most marked. Experimental inoculation with tuberculosis has shown that the inbreds were inferior, on the average, to the controls in disease resistance. A study of sex ratio yields results in marked contrast to those obtained in connection with the other characters. There are no significant fluctuations from year to year, no contrast between inbreds and controls, and no indications of change due to inbreeding.

In addition to the points brought out in this bulletin, which indicates genetic decline during inbreeding, extensive experiments have been made in which different inbred families have been crossed together. These are described in another paper (*U.S. Dept. Agr. Bull.* 1121) in which it is shown that crossbred guinea pigs born of unrelated inbred parents are distinctly superior to their inbred relatives in nearly all elements of vigor. A slightly larger percentage are born alive, in small litters at least, and a distinctly larger percentage of those born alive are raised. The young are slightly heavier at birth in a given size of litter and gain much more between birth and weaning. They mature earlier, produce larger litters and produce them more regularly than inbreds. Of the young which they produce, a much larger percentage are born alive, especially in large litters, and even more of these are raised than in the first generation. Their young show a further increase in birth weight and in later gains.[1]

It is believed that the results point the way to an important application of inbreeding in the improvement of livestock. Nearly all of the characteristics dealt with here, like most of those of economic importance with livestock, are of a kind which is determined only to a slight extent by heredity in the individual. About 70 per cent of the individual variation in resistance to tuberculosis and over 90 per cent of that in the rate of gain and size of litter are determined by external conditions. Progress by ordinary selection of individuals would thus be very slow or nil. A single unfortunate selection of a sire, good as an individual, but inferior in heredity, is likely at any time to undo all past progress. On the other hand, by starting a large number of inbred lines, important hereditary differences in these respects are brought clearly to light and fixed. Crosses among these lines ought to give a full recovery of whatever vigor has been lost by inbreeding, and particular crosses may safely be expected to show a combination of desired characters distinctly superior to the original stock. Thus a crossbred stock can be developed which can be maintained at a higher level than the original stock, a level which could not have been reached by selection alone. Further improvement is to be sought in a repetition of the process—the isolation of new inbred strains from the improved crossbred stock, followed ultimately by crossing and selection of the best crosses for the foundation of the new stock.

This method of improvement has not been unknown in the past. In fact, most of the recognized breeds of livestock were developed, more or less unconsciously, in this way. Close inbreeding was practiced by the pioneer breeders—Bakewell, the Collings, Bates, Cruickshank, Hewer, etc. The relatively few

[1] WRIGHT, S., The Effects of Inbreeding and Crossbreeding on Guinea Pigs, *U.S.*

promising families and the successful nicks between them were the foundation stock of the breeds. Further development may be expected by the intelligent application of the same principles.[1]

Combining the results described in this and in *Bul.* 1121 there seems no escape from the conclusion that a loss of vigor, especially in fertility, took place as a more or less direct consequence of close inbreeding. The question whether this is an inevitable result of inbreeding, or merely a likely one, as well as other phases of the subject, will be discussed after the presentation of further data.[2]

Hughes[3] has recently reported the results of an interesting inbreeding experiment with Berkshire swine. The pedigree of a litter born in 1931 is shown in Fig. 154.

Inbred litter (8 pigs) Berkshire, Mar. 24, 1931 Univ. of Calif.	Sir Double Leader 2d 350285	Double Leader of U.F. 350282	Double Leader 4th 331377	Enhancer's Leader 2d 318540, Univ. of Calif.
			Double Leader Belle 331378	
		Double Leader Belle of U.F., 350285	Double Leader 4th 331377	
			Double Leader Belle 331378	
	Miss Double Leader Belle 550285	Double Leader of U.F. 350282	Double Leader 4th 331377	Enhancer's Leader Belle 2d 318539, Univ. of Calif.
			Double Leader Belle 331378	
		Double Leader Belle of U.F., 350285	Double Leader 4th 331377	
			Double Leader Belle 331378	

FIG. 154.—Pedigree of inbred pigs.

[1] *Ibid., Bul.* 1121, p. 49.

[2] *Ibid., Bul.* 1090, pp. 31–32.

[3] HUGHES, E. H., Inbreeding Berkshire Swine, *Jour. Hered.*, **24** (5): 200, May,

It is evident from the pedigree that full brother-sister matings were made for four generations; *i.e.*, there are only two animals in each of these four generations. Enhancer's Leader 2d and Enhancer's Leader Belle 2d were by the same sire, Enhancer, and out of half sisters by the same sire. There is enough additional inbreeding further back in the pedigree to give these pigs a total inbreeding coefficient (Wright) of 74 per cent.

Hughes gives the following summary of the results thus far achieved:

1. The average number of pigs farrowed, in the inbred litters, has been greater (9.78 pigs per litter) than the average for the Berkshire herd (8.14 pigs per litter for the years 1919–1926).

2. There has been a slight but gradual decrease in the number of pigs farrowed in the inbred litters since 1923. The last litters, however, were the first litters of the sows in question, which tended to be smaller.

3. The type of the pigs in all the inbred litters has been similar.

4. There has been no noticeable color change or structural abnormalities in any of the inbred pigs.

5. The results obtained thus far seem to agree in part with those of Miss King (no noticeable loss in size or vigor) and in part with the results of other workers (there has been a slight decrease in size of the inbred litters).

6. The standard deviation from the mean of the inbred litters is 2.56 with a probable error of ± 0.288. The standard deviation from the mean of all Berkshire litters from 1919 to 1926 inclusive is 5.34 with a probable error of ± 0.302.

Woodward and Graves inbred grade Guernsey and grade Holstein cattle—females mated back to their own sire for successive generations, etc. In the Guernseys the birth weights declined, some deformities appeared, mature weight declined, amount of milk production remained about the same, fat percentage increased. In the Holsteins, birth weights declined, vigor declined, mature weight declined—amount of milk production increased, fat percentage decreased.

Bartlett, Reece, and Mixner have inbred Holstein cattle at the New Jersey Agricultural Experiment Station with lethals and deformities appearing in some families, very poor type and red color in other families, good results in some families. They stress the point that rigid selection must be practiced along with inbreeding.

Use of Inbreeding.—Inbreeding has been used very little in animal breeding up to the present. Bakewell practiced inbreeding to some extent in England during the eighteenth century, and, when other breeders took up the practice, the foundations for our present breeds were laid. During the past 100 years, however, little animal inbreeding has been practiced. The larger and more influential breeders have used inbreeding to a limited degree, but the belief that there is something

inherently harmful in inbreeding plus the justified prohibitions against it in the human have greatly restricted its use, and in consequence many possibilities of more rapid progress in breeding were lost.

In 1905 G. H. Shull at the Station for Experimental Evolution of the Carnegie Institution at Cold Spring Harbor, N.Y., and E. M. East at the Illinois Experiment Station began the experimental inbreeding and hybridization of corn. This work has now developed to the point where the majority of field corn produced in the corn belt is "hybrid" corn. The procedure involves the inbreeding of corn for seven or eight generations, by which time the strain is practically pure or homozygous. Rigid selection is practiced, and the weakest strains discarded. There is always a decrease in yield in these inbred strains. After the best surviving strains have been purified by inbreeding, they are crossed, hybridized, in an experimental way to determine which inbred strains best complement each other. Many systems of hybridizing are in use including the single cross between two inbred strains, the three-way cross of a third inbred on the result of crossing two other inbred strains, double crosses between two single crosses involving four inbred strains, and top crossing of an inbred strain on a commercial variety. All of these systems have certain advantages and disadvantages, the double-cross system being the one most generally practiced.

This hybrid corn has been compared with the mule hybrid in animals. Both of them are excellent in themselves but genetically poor from a breeding standpoint, the mule of course seldom being fertile anyway. Only the first generation of hybrid corn should be used for commercial planting, as the second generation generally drops in yield by from 10 to 25 per cent. Properly produced and tested hybrids that are carefully selected for their adaptability for certain regions will yield on the average about 8 to 10 per cent more than commercial seed-corn varieties.

The corn breeder is thus analyzing his materials, finding out what they are genetically through inbreeding and record keeping, and trying to fit these known strains together into superior strains. He, of course, has a big advantage over the animal breeder in that self-fertilization can be practiced, making the inbreeding twice as intense as is possible with animals, his number of offspring is many times that possible with even the most prolific animals, and the cost of producing a corn plant is much less than that involved in producing a colt, calf, lamb, or pig.

During the past few years, however, regional animal-breeding laboratories have been established by the U.S. Department of Agriculture in various parts of the United States. Inbreeding experiments with animals as closely comparable with the corn experimental inbreeding work as the difference in the materials permit are now being started. Only with such a setup would it seem to be possible to do the things that are neces-

sary to place our animal breeding on a sure scientific foundation; *viz.*, by discovering the true genetic make-up of our livestock by inbreeding and record keeping, after which it should be possible to create more efficient, more beautiful, and truer breeding strains.

The man with just average livestock should, of course, not practice inbreeding. The fact that his stock is average means that it has a goodly share of undesirable genes, which inbreeding would make homozygous and therefore worse. For average livestock, outcrossing would seem to be a better system, for unrelated animals would have less likelihood of carrying identical poor genes.

The man with better than average livestock should do some inbreeding. The fact that his stock is above the average merit of the breed means that a random selected unrelated animal will have a tendency to pull his herd or flock back toward the breed average. Since many breeders still shy at the word inbreeding, we will say that the better than average breeder should practice linebreeding, which of course is a form of inbreeding, but a term which does not have the same fearsome connotations as inbreeding.

Every breeder should try to buy his males in the best available family in his breed. In the present state of our knowledge, the genetically best families in any breed are not easy to know, and one must be wary of advertising and "ballyhoo." Assuming one does buy a sire in a really good family, then, generally speaking, he should try to stay in that family, intensify its good qualities through linebreeding, and weed out the poor genes.

Linebreeding.—This is a term which apparently is sometimes misunderstood. It is not necessarily measured by an inbreeding coefficient, as is illustrated in Fig. 155.

Three of the pedigrees in Fig. 155 show the same amount of inbreeding, but the percentage of "blood" from a certain animal is very different. If we are ever fortunate enough to own a really good sire, we will want to keep his inheritance as intact as possible in our herds.

If we have a good sire, B, his offspring are good presumably, because they get one-half of their inheritance from B, in other words, B's inheritance has been halved just once.

Now, if we get another sire A, unrelated to B, then

A's offspring or B's granddaughters	A	X
		Y
	B's offspring	B
		Foundation animals

B's inheritance has been halved once more; it is only one-half as strong now, and will continue to be further diluted if we use lines unrelated to B.

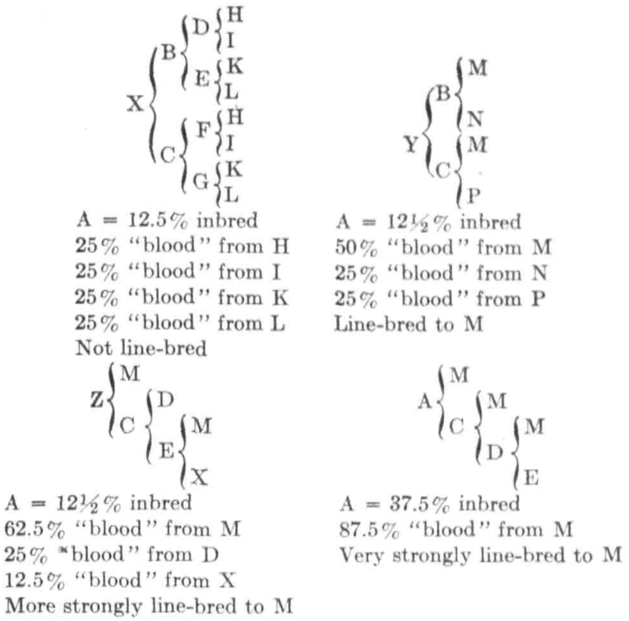
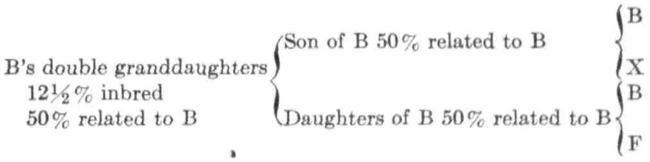


FIG. 155.—Pedigrees to illustrate line breeding.

When we get a good sire, we should try to keep our herd related to him as much as it will stand, and this, of course, involves some degree of inbreeding. The following diagram illustrates how a herd or flock might be made to retain its 50 per cent relationship to a good sire B.



It is evident that the above scheme involves some inbreeding, actually some linebreeding. Each animal born is unique as far as genetic make-up is concerned; *i.e.*, there never has been, nor can there ever be, another animal with an identical genetic make-up. When a great sire dies, we can only retain a degree of relationship to him as strong as the relationship evidenced by any of his living descendants. If we have animals that are 50 per cent related to him and mate them, the herd will remain 50 per cent related to the original good sire, but this relationship to him cannot be increased after he has died. If we have animals that are 75 per cent related to him and mate them, the herd will continue to be 75 per cent related to the good sire. Even five generations of breeding sire to

his daughter will only give us an animal 96.875 per cent related to the original sire.

Conclusion on Inbreeding.—From the foregoing, one is forced to conclude that inbreeding in itself is powerless to create either good or bad. If good or bad is present in the germ plasm, inbreeding will sort it out and bring it to light. Closebreeding may be used in the better herds and flocks if accompanied by very rigid selection. However, linebreeding, a less intense form of inbreeding, is decidedly safer. This consists of mating animals of the same general line of descent. Because they are of the same line, they have the same general type of germ plasm and so exhibit the same general set of characteristics. In other words, a linebred herd or flock is extremely uniform, a characteristic almost invaluable (if of a good sort) in animal breeding. In a general way, closebreeding has the greatest possibilities both for good and for harm, whereas outbreeding or mating of animals of no degree of kinship has perhaps the least possibilities for good and the least danger of producing harmful results. It is conceivable, of course, that two animals showing no pedigree relationship for several generations back might have identical genes for one or more characteristics or potentialities, and, that if these two animals were mated, it would, as far as their like genes are concerned, be tantamount to inbreeding.

If the breeder is keen enough in mating his animals and severe enough in culling, he may practice closebreeding. Such pioneering requires both courage and skill. The majority of breeders ought perhaps to seek the middle road, the happy medium. Their desire is to progress, but they cannot afford to take great chances. For such breeders, both their hope and their safety lie in linebreeding, which is an attempt to secure a greater degree of homozygosity of certain desirable genes without running too great a risk of intensifying undesirable ones. This result can be accomplished in a variety of ways.

It is perhaps easier to linebreed to an outstanding male rather than to an outstanding female because of the greater number of offspring of the former. If one found himself in possession of a really great sire (proved great by his offspring) with many sons and daughters of this sire, he could select two or more of the best sons to mate with the daughters, balancing defects, if present, in the particular matings made. The next generation could be formed by mating the daughters of one sire to a son of another, etc. There is, of course, some danger in the first matings of half brothers and sisters, but, if this stage is passed successfully, there should be no great future danger. The second generation would be double grandsons and granddaughters of the original sire, and the third generation would be quadruple great, great grandsons and daughters of the original sire. The fourth generation and later ones

would also show some inbreeding to the sons, grandsons, etc., of the two original sons used. These amounts are very small, however. This system should gradually render the genes from the original sire more homozygous, and in general half of the genes of the future herd would be those from the original sire. Pearson and Lush[1] have recently pointed out that essentially this system is being used with marked success by Mr.

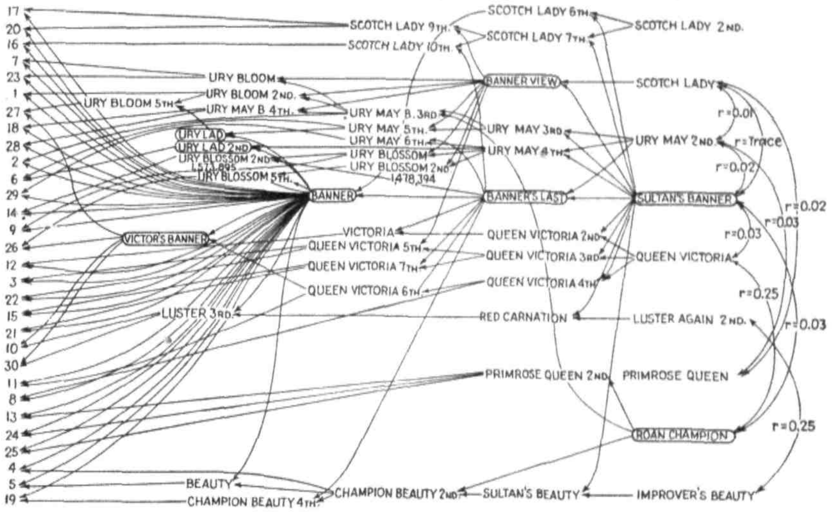


FIG. 156.—Five generations of inbreeding. Pedigree of the entire young herd late in 1932 complete back to the time of Sultan's Banner, and with coefficients of relationship (r) based on the ancestors alive in or near 1900. Each animal is shown but once. If it has more than one son or daughter, an additional arrow indicates that. Selection has not yet had much opportunity to thin out the young herd. When that inevitable culling takes place many of the lines from Banner will disappear. In the herd ten or fifteen years from now, even though the present plan is continued, Banner may not appear much more important than Bannerview or Banner's Last. In any case he is not apt to be more important that those two combined. (*From Lush, J. L., A Herd of Cattle Bred for Twenty Years without New Blood, Jour. Hered.*, **25** (6): 209–218, *June*, 1934.)

C. C. Good of Ogden, Iowa, in his breeding operations with Belgian horses.

Lush has reported on a herd of beef Shorthorn cattle bred for 20 years without new blood "with the merits of the early good ancestor reasonably well conserved, with the whole herd nearly as like each other genetically as ordinary full sisters, and with the herd still maintaining a reasonably high average of individual merit."[2] A composite pedigree of this herd is shown in Fig. 156.

[1] PEARSON, P. B., and LUSH, J. L., A Linebreeding Program for Horse Breeding, *Jour. Hered.*, **24** (5): 185, 1933.

[2] LUSH, J. L., A Herd of Cattle Bred for Twenty Years without New Blood, *Jour. Hered.*, **25** (6): 209–218, June, 1934.

Another system of linebreeding would result from mating the daughters of a sire to a son of the same sire but out of an unrelated dam, the resulting daughters to be mated to a son of the sire of the daughters again out of an unrelated dam. In this way one is always mating half brothers and sisters and producing double granddaughters of certain bulls. However, outside "blood" is being introduced by selecting the sires from unrelated dams. Various other types and combinations of linebreeding systems are, of course, possible, the aim in all of them being to intensify certain characteristics by rendering them homozygous, at the same time weeding out the homozygous undesirable characteristics. The success or failure of any system of breeding lies first in the genes that the original animals have and second in the breeder's ability to balance defects and mate wisely—in other words, his ability to select.

Purebreds have existed for many decades. They have, of necessity, been bred more or less closely, so that inbreeding is perhaps not so necessary now as it was in founding the various breeds. The aim of the constructive breeder, however, is to find the best and most prepotent "blood" in his breed, to secure a worthy sire carrying that blood, and then to intensify this blood through some form of inbreeding. Finally, let us remind ourselves once more than any system of breeding is simply the means to an end and not the end itself. Whether this or that system of breeding will prove efficacious in achieving some particular end depends upon the make-up of the genes, as well as upon the system of breeding employed.

Summary.—We have seen in this chapter that animals which evidence relationship by having common ancestors within the first four to six generations of their pedigrees are likely to have received identical genes from their close-up common ancestors. When two such related animals are mated, they may both pass their identical genes to their offspring. Matings involving related animals are called *inbreeding*, and an inbred animal is likely to be homozygous in more sets of genes than is an outbred animal. Inbreeding creates no new genes but allows those already present to get into homozygous combinations. Inbreeding results in improvement or deterioration depending entirely on the genes present in the related animals. Only those breeders whose herds are fairly large and of more than average merit should practice closebreeding. Linebreeding should have a greater vogue than it has had in the past.

Inbreeding will be successful (1) if the good genes pretty well outnumber the bad ones to start with, (2) if the breeder has more than average skill in planning his matings, (3) if the breeder can and will practice very rigid selection. Finally, it isn't the system of mating—it's the genes in the animals and the intelligence in the man, and the latter is also largely a matter of genes.

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[1] See also Appendix A.

CHAPTER XXII

GENERAL CONSIDERATIONS IN SELECTION

Selection is the keystone of the arch in animal breeding. The fact that a breeder's ultimate success depends upon his skill in selecting and mating animals is so obvious that it permits of no argument. It will be recognized immediately also that selection and systems of breeding are bound together so closely that there is no likelihood of being able to separate them. They are but different angles of this same basic problem. We have seen that an animal's ultimate and intrinsic worth depends in the final analysis on the genetic contents of the egg and the sperm that united to produce it. We must, therefore, relate all of our thinking about selection to the ultimate determiners of potentialities—genes and chromosomes—and it hardly seems necessary to add that whether or not an animal with a good hereditary complex actually develops into a desirable individual depends in turn on the type of environment, especially feed, care, and management, which is provided. If our selection is successful, if the animals we breed, in other words, are superior in the qualities that enable them to perform their respective functions successfully and profitably, it will be because their good genes have had an opportunity to express themselves in a good environment.

Selection is nothing new. It has been going on for over a billion years, or since the first forms of life appeared on this planet. This is called *natural selection* and is the idea on which Charles Darwin formulated his theory of evolution. For millions of years before man even appeared on the scene, "Nature" was busy putting the genes together into new combinations (variations). Some of these new combinations were successful, giving rise to new types of life that were adapted to the given environment. They, therefore, prospered and multiplied. The unsuccessful combinations were those giving rise to animals that were ill-adapted to their environment. They could not live and prosper and therefore left few or no progeny. "Nature" was ruthless, her one criterion was fitness, and on the dual bases of variation and fitness she has peopled the earth with myriad forms of life. A long, long succession of successful variations finally produced man himself, a creature of sublime potentialities, most of which are yet to be achieved.

One of man's early and most far-reaching accomplishments was the domestication of plants and animals. When this had been accomplished, Nature's passive selection was supplanted by man's active *artificial*

selection. The latter has been going on for some 5,000 to 10,000 years; and, in spite of certain cynical opinions to the contrary, it has had a truly remarkable degree of success. For proof of this statement, all we need do is contrast a wild boar and a champion barrow; a Texas Longhorn and a grand champion steer; a mouflon and a modern sheep, Przhevalskis horse and a modern Percheron; an early type cow and a modern dairy queen. Both in looks and utility such a wide gulf separates these extremes that one marvels it could be bridged in such a short space of time. Some critics aver that there has been no progress in livestock breeding during the past 200 years, that all our gains in animal form and function are due to better feeding and management. That the latter have played a large part no intelligent person would wish to deny, but to give them the whole credit seems just a bit "assinine." It is tantamount to saying that all livestock breeders' efforts at selection have been fruitless, that as a group they have not increased to any degree the relative frequency of good genes or been able to discard any bad ones.

If one wishes to maintain that selection methods have not been 100 per cent efficient, he would have ample justification for his position, but to deny any progress in breeding for the past two centuries is simply not in keeping with facts, and before being too critical of breeders of the past one should, in fairness, recognize the handicaps under which they worked. The mechanism of reproduction was the last field tackled by the physiologist, and its complete functioning in terms of the immediate organs concerned and the remote controls situated in the endocrines is only now beginning to be understood in a relatively complete manner. Likewise the mechanism of hereditary transmission has been understood for only 40 years, and its real use as a tool in creating better plants and animals was begun only 20 or 30 years ago. Mass or phenotypic selection has brought us a long way from the crude and inefficient types of animals with which man began his task. It can be admitted that "ox-cart" or "horse-and-buggy" methods of selection need modernizing without belittling the accomplishments and tools of those who have passed on.

For a long time, selection in all classes of livestock was based upon individual appearance, that is to say, ideals of bodily form were set up after which the breeder tried to mold his own herd or flock. Many influences helped to shape these ideals, one of the most important of which was the show-ring standard. It was thought, in other words, that there was a relation between form and function with horses and dairy cattle as well as with meat animals. Selection was based largely on anatomy. Gradually, however, it became apparent that, in dairy cattle especially, there was no necessary correlation between type and production, between external anatomy and internal physiology. Selection then shifted its base somewhat by including a consideration of

performance at the drawbar, at the milk pail, or in the feed lot. Selection, in other words, came to include physiological functioning as well as anatomy. Finally, however, it became apparent that an animal's own performance was no safer guide to its transmitting ability than its anatomy had been of its own scale of performance.

In recent years, therefore, we have heard much of progeny-performance tests as the only safe measure of an animal's breeding merit. We still pay attention to type, anatomy, or external appearance; we still pay attention to performance, physiology, or internal activity; but to these criteria of selection we have now added a consideration of how the animal actually performs in transmitting its own desirable qualities. We pay no less attention to individual appearance or individual performance than we formerly did. We want both these things in our breeding animals, but we have slowly come to realize that having either one or both does not guarantee that an animal will be a good transmitter. If we can make our animals' pedigrees complete enough in terms of records of accomplishments (both as individuals and as transmitters) of the direct ancestors in the pedigree and a goodly share of the collateral relatives, we can predict with a fair degree of assurance how the animals will transmit. However, the final and only sure test of an animal's breeding worth is now recognized to reside in the quality of its offspring. Good type, good performance, good pedigree (in terms of records) are indications of breeding merit, but the only assurance of breeding merit resides in the offspring themselves.

Erroneous Notions about Selection.—There have been many superstitions about selection that would make an interesting and somewhat humorous discourse, but at the same time this would serve no practical purpose. One fallacious idea, however, merits some mention. It arose from the early success of selection in molding animal and plant types toward an ideal and led to a belief that selection had practically no upper limit. The discovery of the hereditary mechanism as resident in the genes finally dispelled this illusion. This was brought about largely through the work of Johannsen with the self-fertilizing garden bean. From a mixed population, he selected plants that bore large seed and others that bore small seed. Attempts at selection within these "pure lines," however, proved unavailing. Selecting large seed from the large line gave no larger seed on the average than did small seed from this line. Likewise the selection of small seed from the small line gave no smaller seed on the average than did large seed from the small line. Johannsen designated these as "pure lines," *i.e.*, pure from a genetic standpoint. Small seed from the large line was small because of environmental effects, but genetically these small seeds were just like the large seeds in the same line.

Selection, therefore, did prove to have an upper limit, and selection within a "pure line" was not effective. Thus, for the first time, it was fully realized that the effectiveness of selection was entirely dependent on the nature of the hereditary units. If a quantitative character depends on two sets of genes *A* and *B* and we start with a heterozygous generation *Aa Bb*, we can get out a line that is *AA BB* or *aa bb* thus showing the character to a greater or less degree than did the ancestors. When we can get a line that is *AA BB*, thus showing the character to a greater degree, we cannot go beyond this point. This is a pure line which under optimum environmental conditions will always breed true.

This general principle is applicable to all living forms. In our livestock, it is probable that most commercially desirable characters are of a quantitative sort and probably controlled by scores or hundreds of genes. What we are attempting to do in selecting is to develop our animals into "pure lines" or as close to this as we can get with unisexual animals. The task is not an easy one because of the time necessary and the complications involved in dealing with large numbers of genes, but knowing the underlying scientific basis will at least enable us to chart our course more intelligently. Dealing with large numbers of genes simply means that it will take a long time to get them sorted out into the desired homozygous forms, but we can have the comfort of knowing that when we once get them sorted out they will remain in that condition indefinitely except for an occasional mutation.

This brings to mind the importance and gravity of the decision to introduce a certain male into our breeding plans. When once we bring a male into our herd or flock, his influence, good or bad, is apt to remain with us for some time. When once his genes are put into our "hereditary mix," they remain there more or less indefinitely. Probably most males will bring in some undesirable genes, and, if there are not too many of them, we can hope to rid ourselves of them in a reasonable length of time. If a male brings a host of bad genes, they may plague us through many generations.

Changing Gene Frequencies.[1]—Since genes determine characters, breeders, in selecting for certain things, are actually trying to influence the proportion of different genes in their stock. Wright, in studying the coat colors of the parents of 3,000 Shorthorn cattle, found that 47.6 per cent were red, 43.8 per cent were roan, and 8.6 per cent were white. Since this is a character seemingly controlled by one pair of genes lacking dominance, we know that to the 8.6 per cent of white genes showing as white and to the 47.6 per cent of red genes showing as red must be added one-half the roan value 43.8/2, or 21.9 (roan being *RW*), in order

[1] See LUSH, J. L., "Animal Breeding Plans," pp. 53–60, Collegiate Press, Inc., of Iowa State College, Ames, Iowa, 1937.

to get the frequency of the white and the red genes in the population. Thus, 47.6 + 21.9 = 69.5% red genes and 8.6 + 21.9 = 30.5% white genes in the population. Now, if the population had been mating at random, we would have had

	69.5 *R*	30.5 *W*
69.5 *R*	48.3 *RR*	21.2 *RW*
30.5 *W*	21.2 *RW*	9.3 *WW*

or

48.3 *RR* : 42.4 *RW* : 9.3 *WW*

instead of

47.6 *RR* : 43.8 *RW* : 8.6 *WW*

This slight discrepancy shows that mating was not at random but that there was a preference on the part of breeders for roan.

Generally q is used to represent the frequency of one gene and $1 - q$ its allele, and since in random mating the proportion of different zygotes will be the square of the gametic ratio, the ratio of zygotes becomes:

$$q^2 : 2q(1 - q) : (1 - q)^2$$

If either the first or the last term is known, the others can be computed. If 1 per cent of Holstein calves were born red in color, then red, *rr*, or $(1 - q)^2 = 0.01$ and $(1 - q) = 0.1$ and $q = 0.9$. So under this assumption 81 per cent of Holsteins would be pure for black, homozygous *BB*; 18 per cent heterozygous, *Bb*; and 1 per cent would be red. In other words, if 1 per cent of Holstein calves are born red, then 1:5 or 6 black Holsteins are heterozygous for color.

This principle applies also to independently segregating, nonallelic gene pairs. This can be shown by the usual 9:3:3:1 dihybrid ratio. If genes *A* and *a* have a frequency of 0.5, genes *B* and *b* also a frequency of 0.5, then they will recombine as shown in Fig. 157.

	q^2 *AA* 0.25	$2q(1 - q)^2$ *Aa* 0.50	$(1 - q)^2$ *aa* 0.25
q^2 *BB* 0.25	0.0625 *AA BB*	0.1250 *Aa BB*	0.0625 *aa BB*
$2q(1 - q)$ *Bb* 0.50	0.1250 *AA Bb*	0.2500 *Aa Bb*	0.1250 *aa Bb*
$(1 - q)^2$ *bb* 0.25	0.0625 *AA bb*	0.1250 *Aa bb*	0.625 *aa bb*

Fig. 157.—Independently segregating genes *A* and *B*, frequency = 0.5

This formula could be extended to n genes by serial multiplication of the squared binomial of each independently segregating gene, $[q_A A + (1 - q_A)a]^2[q_B B + (1 - q_B)b]^2$, etc., to n.

Thus we can see that with two pairs of genes of equal frequency (0.5) we would have 1:16 chances of getting an animal pure for both pairs of dominant genes (*AA BB*). This chance, assuming usual gene frequencies, is calculated according to the formula q^{2n} (n being the number of pairs of genes involved). Thus, in Fig. 157, q was 0.5 and n pairs of genes was 2, so $0.5^4 = 6.25\%$, or 1:16 chances. With q at 0.4 and five pairs of genes, we would have $0.4^{10} = 0.0001$, or 1:10,000 chances of getting an animal homozygous for all five pairs of genes whose frequencies were 0.4. If the gene frequencies had been 0.6, our chance would have been 1:166; if it had been 0.8, our chance would have been 1: about 100; whereas, if the gene frequencies had been 0.99, we would have had 1:1.1 chances. That is, if a herd was almost all *AA* with very few *Aa* or *aa*, *BB* with very few *Bb* or *bb*, *CC* with very few *Cc* or *cc*, etc., it would not be difficult to keep them *AA*, *BB*, *CC*, etc.

It is obvious that increasing the number of gene pairs being selected for reduces the chances of securing them all in a homozygous state. If we increase the pairs to 10 and leave the frequency at 0.99, our chance of success drops to 1:1.2, whereas increasing gene pairs to 20 reduces our chance to 1:1.5 and increasing the gene pairs to 50 reduces our chance of success to about 1:3. In practice the more things we try to select for simultaneously, the more likely we are to fail. In our college dairy herds, we feel that we must have both good type and good production. The genes, however, that bring about style, straight tops, fine withers, well-set legs, etc., do not necessarily have anything to do with the physiological functioning of the organs and glands that result in a heavy milk flow. If we could select for production alone, we probably could get it more quickly, and we might also get ewe necks, weak backs, sloping rumps, pendulous udders, crooked legs, etc. If one-third of the animals in any dairy breed would suit us from a production standpoint and one-third of them from a type standpoint and these two things were not closely correlated, then it is obvious that only one-ninth of the animals of the breed would suit us from combined standpoint of type and production. The more uncorrelated things we select for simultaneously, the more we narrow our range of selection and the more we reduce our chances of success.

It is apparent that it would be easier to find an animal having at least one of the desired genes than it would to find one having both, since, if q^2 are *AA* and $2q(1 - q)$ are *Aa*, then those which have at least one *A* are $q^2 + 2q(1 - q)$, or $2q - q^2$, which may be written $q(2 - q)$. This can also be extended to n pairs of genes by applying the formula $q(2 - q)^n$. Thus, in our last example of a dihybrid with equal gene frequencies, we

would have $q(2 - q)^n = 0.5(1.5)^2 = 0.75^2 = 56.25\%$, or 1:2 chances of getting an animal that had at least one A and one B. With q at 0.4 and 5 pairs of genes, we would have 1: about 100 chances of getting an animal with at least one dominant gene in all the five pairs involved; whereas, if the gene frequencies had been 0.6 for each of the five pairs, our chance would have been 1:2.5; at 0.8, it would have been 1:1.2; at 0.99, it would have been 1:1.0005, or a practical certainty. Lowering the gene frequencies or increasing the number of pairs of genes involved curtails the likelihood of selection being successful.

From the above discussion and in view of the fact that most of our animals are still relatively heterozygous (gene frequencies around 0.5) for many pairs of genes and that most of the commercially desirable qualities are probably controlled by many (perhaps 20 or 100) pairs of genes, the breeder's task is seen to be very difficult and complicated. With intelligent selection, however, based on recorded data, he can favorably influence gene frequencies in his herd or flock. He may never render his animals homozygous for all the desirable genes, but he has the assurance that the merit and value of his animals will increase with the increasing frequency of desirable genes.

It is obvious also that selection for a recessive is much more simple than selection for a dominant owing to the fact that, if dominance prevails, then AA and Aa animals are indistinguishable phenotypically, while the aa animals can be recognized genetically from their phenotype. The Suffolk horse is a good example of this, its color, chestnut or sorrel, being due to a pair of recessive genes, this being the only color found in the breed. If early importers and breeders of Holsteins had elected the red and white instead of the black and white color pattern, they would not have been plagued with off colors that often lead to suspicion of the purity of breeding of the animals producing them. When a red calf is born in an Angus or Holstein herd, the sire and the dam are, of course, jointly and equally responsible, each having transmitted the recessive gene. With 1 calf in 100 born red, the genetic make-up of the breed is 81 per cent BB, 18 per cent Bb, 1 per cent bb (red).

Just to weed out the reds as they are born will have little effect on purifying the breed for color, since 90 per cent of the b genes are hidden in Bb animals, while only 10 per cent are visible in bb animals. If we started with an F_2 generation that was 25 per cent BB, 50 per cent Bb, and 25 per cent bb, it would take eight generations of eliminating bb individuals to get the proportion down to 1 per cent bb animals, or 1:100; whereas to halve this amount, *i.e.*, make it 1:200, would require four more generations; to get it to 1:400 would require six more generations; and to get it to 1:800 would require eight more generations. This sort of mass or phenotypic selection is seen to work very slowly. It can be greatly

hastened, of course, by discarding any animals that have offspring showing the undesirable recessive character and also those whose sibs, cousins, or other collateral relatives show the character, in other words, by adding genotypic selection to the phenotypic.

Most of the problems and examples used to illustrate genetic principles involve a very few sets of alleles. The student and breeder needs, therefore, to remind himself constantly that this is, in general, an oversimplification. It is known, for instance, in the pomace fly *Drosophila melanogaster* that upward of 40 genes function in producing the wild-type eye color of red. If 40 of these pairs were the necessary dominant genes but the forty-first pair had mutated to, say, garnet, then the eyes would be garnet instead of red. Some of these 40 odd pairs of genes are located in each of the 4 pairs of chromosomes.

In our domestic animals, there seem to be 20 to 30 pairs of chromosomes with perhaps 100 or more genes in each chromosome. What we are actually dealing with therefore, from a practical standpoint, would seem to be a complex gene complex. We talk about individual genes, but we actually are dealing with blocks or groups of genes. It may be possible too that in a certain gene complex, the homozygous dominant AA serves best, while in another perhaps Aa does, and in still another perhaps the homozygous recessive is best. As we have said previously, the breeder is attempting by selection to put together the best possible gene complex, to influence the proportion of desirable genes in his stock in a favorable manner, and he uses a variety of criteria to measure the value of the gene complexes that he has or desires to get.

Gene frequencies for various qualities are quite variable both in and between various breeds. To take an extreme example, the genes making for the type and temperament associated with speed are very scarce in the Percheron breed of horses. Nevertheless, there are probably enough of them present so that many generations of selection for these genes would make them sufficient in number to produce a horse of considerable speed. Similarly the genes for red color are very few in the Angus breed, but constant selection for them would result in changing the breed from black to red. And in Holstein cattle the genes for higher butterfat test (4 to 5 per cent) are relatively scarce, but enough of them exist so that selection over many generations could result in an average test for the breed of over 4 per cent.

Heredity vs. Environment in Selection.—The past has seen many arguments between the hereditarians and the environmentalists, with first one and then the other having seemingly the better of the argument. The debate has of late tended to be resolved by the simple but far-reaching expedient of substituting *and* for *vs.* In other words it is not a case of whether heredity *or* environment is the most important. Both are

important, one just as much as the other. Neither good genes and a poor environment nor bad genes and a good environment will give us a profitable and satisfactory animal husbandry. We must have both.

There is still a considerable problem in this field, not the old one of attempting to determine which is the most important, but rather that of perfecting devices that will measure the influence of the two in a given case. Obviously some characters like color pattern are largely hereditary, owing to the genes. Others like milk in the pail or fat on the carcass are determined both by the genes and by environmental factors—feed, care, etc.

The problem, then, is to determine the relative importance of the genes and the environment in bringing about differences in animals. These differences are generally expressed by the term *variance*, which is the square of the standard deviation, or the average of the squared deviations of the individuals (σ_0^2) concerned from the average or means of the population. Since the total variance is made up of both the hereditary (σ_H^2) and environmental (σ_E^2) we could find the percentage due to heredity by the formula σ_H^2/σ_0^2, the remaining portion being due to the environment. Wright has done this for the amount of white spotting in stocks of inbred and outbred guinea pigs, with the result that 97.2 per cent of the variance in the homozygous inbred strain was found to be due to the environment, whereas only 57.5 per cent of that in the outbred strain was environmental. Other investigations show various proportions between heredity and environment, with heredity seldom getting up to as high as 50 per cent. We can conclude, therefore, that both heredity and environment are important, although for certain characteristics one perhaps is more important than the other.

The breeder's task is to determine to the best of his ability how much of the variance in any given case is due to environment and to make due allowance for it in practicing selection. This is necessary because, as we have already learned, only the hereditary variations are capable of being passed along to an animal's progeny. If a group of heifers in comparison with their dams had better feed and care, calved at a more advantageous season of the year, were better fed while milking, were not bred as soon after freshening, etc., with the result that they considerably exceeded their dams' production, it would obviously be unfair to attribute all this excellence to their heredity. Better or worse feed, weather, and other environmental conditions could make a considerably difference in a crop of lambs or pigs even though there were no appreciable genetic differences.

At present, the breeder has no practical tools for separating the genetic from the environmental causes of variation except his own judgment applied to individual cases, and his judgment unsupported by

factual material in the form of carefully kept records is liable to be untrustworthy. If he will keep records, however, and appraise them intelligently and fairly, not letting his judgment be warped by individual likes and dislikes in regard to his breeding animals, he will be well on the way to avoiding the all too common mistake of assigning to heredity what rightfully belongs to environment. His success or failure depends to a large extent on his ability to do just this, for the simple reason that hereditary differences may be transmitted, whereas environmental ones apparently cannot be transmitted.

The Market and Selection.—The ultimate purpose for which animals are bred is that of supplying the needs and desires of consumers. The market pays more for a low-set, blocky, well-finished, and marbled steer than it does for an upstanding, narrow animal in thin condition, because the former satisfies the wants of the consumer to a greater degree. Horses of accepted draft type and cows of dairy type will command higher prices than animals lacking these outward appearances, because the buyer feels that they are better equipped to perform their respective functions. The breeder, therefore, should be a careful student of market demands. Coupled with this should be a careful scrutinizing of his records in order to ascertain the type of animals that actually returns the greatest profit to the breeder, because the animal that brings the most money on the market is not necessarily and always the one that nets the breeder the most profit.

Most breeders must make their living through selling the animals they breed or the products therefrom. The mere fact that they have produced efficient and attractive animals will not of itself prove profitable if the market does not happen to be in the mood to buy that particular sort of animal or product. The breeder who is to get ahead must be a keen student of what the market demands and is apt to demand in the next few years. This should not, in the slightest degree, be construed to mean that breeders should follow every whim of the market and be continually attempting to change type. Such practice can lead to nothing but chaos. The successful breeder is the one who can sense the difference between a passing whim and a permanent change. The market is not a fixed institution incapable of change. For substantiation of this, one need but refer to pictures of accepted animal types of 20 years ago and to consult market statistics of two decades past. The progressive breeder senses each change somewhere near its beginning and shapes his course accordingly. In so doing he begins to practice selection for the new type one or a few generations before his fellow breeders and generally reaps a financial reward for his shrewdness and foresight. He also, of course, runs the risk of guessing wrongly—for which he probably will pay a penalty.

What type changes in draft horses will be expedient or necessary in view of the increasing use of tractors? What type changes would be desirable in dairy cattle owing to the likelihood that we will want to feed them an increased (or decreased) proportion of roughage? Will a changing feed situation, new knowledge of the functions of the endocrine glands in growth and fattening, or possible adjustments in our system of governing ourselves make somewhat different types of meat animals desirable? "Ty" Cobb was a great baseball player because he had the imagination to outguess the opposition plus the skill to carry out his plans. He is a great general who outguesses the enemy, a great lawyer who outguesses his adversary in the courtroom, a great scientist who outguesses "nature." Outguessing simply means that the person had curiosity or imagination or vision. For real success the livestock breeder needs more than a sprinkling of this ingredient. Before turning his hand to produce anything, every breeder and farmer should reflect on this most important of all questions, what will the market pay me best to produce? Until that question has been answered, there can be no consistent selection.

Breeds and Selection.—That there are differences between our pure breeds of horses, cattle, sheep, and swine needs no particular elaboration at this point, for they are obvious. They arose because the breeders have followed somewhat different ideals in practicing selection and over a period of time were able to influence the frequencies of certain genes in a recognizable fashion.

There are wide differences both between breeds and between individuals of a given breed. Breed differences may be due to the fact that breed 1 is generally *AA*, whereas breed 2 is generally *aa*. Such differences do actually exist, but they are not now thought to be so important as formerly. Another way in which breeds differ concerns the relative frequency of a given gene within the 2 breeds. Breed 1 may be 90 per cent *AA* and 10 per cent *aa*, whereas another breed may be just the reverse. The genes for high-butterfat test are much more prevalent in Jerseys and Guernseys than they are in Holsteins. This is due largely to selection. Holstein breeders for many years based their selection largely on amount of milk. It is well-known that there is a negative correlation between amount of milk and its butterfat percentage. In other words, in selecting for high milk, Holstein breeders automatically rejected the genes for higher test, so that the Holstein breed now produces a milk with about 3.5 per cent butterfat, whereas Guernsey milk averages about 5 per cent and Jersey milk about 5.4 per cent butterfat. The relative scarceness of the genes for higher test in Holsteins makes the job of developing a 4 per cent herd very difficult. If a breed totally lacked the genes for some desired character, then there would

be no other recourse but to go outside the breed to get these desired genes.

There is nothing in the mechanism of inheritance itself that will change the frequency of any gene in a breed or population. If we start with two animals that are Aa (one-half the genes A and one-half a) and do not select for gene A or gene a, then after any number of generations and with any system of breeding, there will still be as many A genes as a genes in the population.

A stock phrase for many years has been, "There is no best breed," though this statement is only true when there has been added, "for all conditions." There are breeds better suited to certain conditions than are others of the same class, because certain breeds have been grown under, and with a view to fulfilling, similar conditions to the ones now contemplated. Some of our breeds of dairy cattle produce a milk better suited to cheese making or the production of evaporated or condensed milk than do others. Comparable situations exist between breeds of horses, sheep, and swine. Breed tests of various sorts are likely to be very misleading, because in them it is more apt to be the particular strain rather than the breed as a whole that is being tested. If enough so-called "breed tests" were run, no doubt all the breeds would get a share of the winnings. A breeder will find it profitable to make a study of the breeds in order to ascertain which one has been produced under conditions similar to his own and has given the most general satisfaction therein. On the other hand, caution must be exercised in accepting the offerings of overenthusiastic breed advocates. This matter of an unbiased opinion and a thorough knowledge of the breed from its earliest inception to the last sale and showyard winning or loss cannot be overstressed. Such knowledge is essential before a pedigree in the breed can be properly evaluated.

Each of the breeds has certain exterior trade-marks that make it possible to differentiate the breeds without any serious likelihood of error. In this sense the trade-marks are an advantage. They may also, of course, be a disadvantage if breeders select for fancy points at the expense of points of utility. In sheep, one breed calls for a long, horizontal ear, others for short, horizontal ears, and others for an erect ear; some breeds demand a very heavy face covering of wool, others a moderate face covering, and still others a clean face; some demand the color markings on face, ears, and lower legs to be black, others brown, others gray, others white; some breeds have no horns, others horns in the male only, others in both sexes.

In swine, some breeds demand erect ears, others moderately erect ears, others lop ears; in some the face must be greatly dished, in others moderately dished, in others straight; some are black colored with a

slight toleration for white, others white with a complete intoleration for black, others varying shades of red, and one requires a white belt to include the front legs and shoulder. The dairy and beef breeds also vary in color, horns, face. The most acceptable colors of Percheron horses, grays and blacks, are not acceptable in Belgians; and the ones the Percherons frown upon, chestnut, sorrel, bay and roan, are the desired colors in Belgians.

The breeds should continually scrutinize these trade-marks. Most of them in themselves are harmless, although some may have positive detriment, horns, face coverings, etc. Reasonable trade-marks should be maintained, but care must be exercised at all times that "the tail does not get to wagging the dog." The principal advantage of the trade-marks is not that they have any intrinsic merit in themselves but that they do enhance uniformity of appearance, and their very existence and recognition reduces the likelihood of fraudulent or careless registration and so helps to protect the purity of the breeds. The existence of separate and distinct breeds has two very important functions; one, in encouraging cooperative effort among men in the same breed; and the other, in stimulating competition among the breeds.

In the choosing of a breed, one must reach a decision as to whether to select a breed already numerous and well-established in the region or to introduce a new and unknown one. Both of these procedures have advantages and disadvantages. If a new breed is chosen, one has the advantage of novelty and monopoly but the very serious disadvantage of standing alone and perhaps being far-removed from other sources of replacement. Conversely, if one chooses a breed that is prominent in the locality, he can have the distinct advantage of other breeders' experience with the breed and the opportunity of wide choice near at hand for his foundation animals and later additions. The good and bad features of other herds in the community are more or less generally known as well as the integrity and dependability of the men themselves.

With the growing trend toward the proving of sires in all classes of livestock, the exchange of good sires in a region in order to extend their use over longer periods of time will probably ensue. Having animals of the same breed as others in the region would allow a new breeder to take advantage of opportunities of this sort. General adoption of such a plan would also tend to create linebred herds in the district, something greatly to be desired in American livestock breeding.

Likewise the trend toward artificial insemination in some classes of livestock would indicate the much greater likelihood of one's being able to have the use of better sires if he were breeding animals in a breed already numerous in a region.

Finally the greater likelihood of developing a market that would attract outside buyers and permit the fostering of consignment sales is an advantage which can grow out of a community's sticking to one breed. Choosing a breed already well-established in a region seems to hold more advantages to the newcomer than the alternative scheme of choosing a breed with few or no breeders in the region.

Individuality and Selection.—What an individual is and does is called its *phenotype*, so that selection based on individuality can properly be called *phenotypic selection*. This has been the most commonly used tool in selection, and to it can be ascribed most of the progress that has been made in shaping nature's imperfect offerings into more efficient and desirable types. Now that the physical mechanism of inheritance is known, we can, of course, better appreciate the shortcomings of phenotypic selection. A polled animal might be of the genetic constitution Pp, which would make it all right from a phenotypic viewpoint but could not prevent such an animal from transmitting the gene for horns (p) to one-half of its offspring. Breeders used to think (and some still do) that they could tell from the appearance (phenotype) of an animal just how it would breed. The informed breeder now knows better than this. He knows that he may learn certain things about breeding abilities from appearances, that he can add to his knowledge from a pedigree which is relatively complete with records and phenotypes of the ancestors, but that actually to ascertain the breeding merit of any animal he must study that animal's offspring, in other words, apply the progeny-performance test.

All these considerations are important, though there can be no question but that the progeny-performance test takes first rank. A good individual and a good pedigree are obviously considerations of great importance. A deficiency in either individual or pedigree is, of course, to be avoided wherever possible. Selection based on individuality alone or on pedigree alone, however, will involve only temporary loss and setback, provided the progeny-performance test is rigorously applied. A thorough study of its physical make-up is essential in selecting an individual to go into the breeding herd. It is here that knowledge of anatomy and practice in judging livestock will stand the breeder in good stead. There can be no question but that livestock shows are the most influential factors in establishing type, and breeders generally would profit by more regular attendance at the leading livestock shows. Like other arts, livestock judging is more or less a gift, but it, too, can be improved through study and practice. The animals that go to make up a herd should be as nearly perfect as possible, but in all animals it is possible to find faults of various sorts. This being true, wise selection will

depend on the breeder's ability to balance one fault or several faults against others and to choose the lesser of the evils.

In selecting foundation animals, it is essential that there be as much uniformity as possible in the band of females. If these are of different types, it will be extremely difficult to get a sire which, when mated with them, will be able to produce a uniform type of offspring. In visiting herds or sales for the purpose of securing foundation animals, one of the cardinal features to be observed and appraised is this matter of uniformity. Uniformity of a good sort is a virtue almost beyond price. One should hesitate, if not entirely refrain, from buying animals out of a flock or herd that evidences samples of all conceivable types. The females, besides being uniform in type, should be of good size in order to facilitate prolificacy and to promote efficiency. The desideratum is as much size as is consistent with quality. Size, however, as well as anything else can be overdone. If the females of any class of livestock are not fairly roomy and stretchy through the middle, the most important feature of all in breeding livestock, *viz.*, fecundity, is apt to be low.

In selecting the sire to mate with a uniform band of good-sized females, the cardinal point to be borne in mind is that he should offset any faults that are present in the females. If the females have a tendency to sloping rumps, the male should be particularly strong and level in this respect, as well as being a member of a family strong in this regard; if they show weak pasterns, he must stand well up on his toes, etc. If size and vigor are present in the females, one can logically accept a little more compactness and quality in the male, especially if producing meat animals. In the sire, there should be evidence of masculinity, but it should be remembered that this is often overdone at the expense of quality. Breed history, both good and bad, must also be considered. Particularly is it essential in selecting animals of any breed to avoid those individuals exhibiting the common breed faults, such as droopy rumps, small teats, etc., in some of the dairy breeds, too fine or too coarse bone in some breeds of horses, undue coarseness in some of the breeds of swine, etc. through all our classes of livestock.

Many breeders base their selection almost wholly upon individuality. This procedure, however, is not genetically sound. The horse that runs well does not always beget fast offspring; the cow that produces well does not always yield high-producing offspring, etc. The reason for this is the fact that every animal has a phenotypic as well as genotypic nature, and the two do not necessarily coincide. Its phenotype determines what the animal looks like and how it performs; its genotype, how it will transmit. For example, there is no way of ascertaining by the inspection of an animal whether it is *BB* or *Bb*. In either case it will be black; *i.e.*, these two genotypes belong to the black phenotype. From a breeding

standpoint, however, these two animals are very different, for they belong to two different genotypes. When mated to red cattle, the first, *BB*, will give all black offspring, whereas the second will give 50 per cent black and 50 per cent red offspring. This is a simple case, to be sure, involving only one pair of genes, but the same reasoning and the same principles apply to the more complex characteristics such as speed, milk production, ability to fatten. It is all right to demand high individual excellence in selecting breeding animals, but it is all wrong to stop with that single consideration.

Dairy cattle breeders have, to some extent, aped the breeders of fat stock and horses and set up arbitrary standards of dairy type. There is a great difference, however, between the selection of beef cattle, for example, and dairy cattle. In the one case we deal with tangibles and in the other with intangibles. The beef animal, male or female, exhibits directly the presence or absence of the desired qualities, *e.g.*, degree of fleshing, width of loin, fullness of round, etc. With dairy cattle, on the other hand, there seems to be little correlation between type and production in the female, and, of course, the bull gives no milk whatsoever. On the face of it, it would seem to be a very naïve assumption that straightness of topline or stylish carriage, for instance, could have any direct bearing on the amount of milk which a cow could give.

It is extremely difficult to tell by looking at a dairy cow how much milk she is capable of yielding. Many of these so-called "guessing contests" have been staged. One was held at the New York State Fair in 1919 which included nine cows ranging in production from 4,454 to 20,852 lb. of milk a year, with about a 2,000-lb. interval between each pair. Over 70,000 people guessed, no one got over five of the cows properly arranged and only 12 people did this well, one-third of the guesses failed to have even one cow in the proper place, and many "guessers" picked the lowest producing cow as the highest producer. So, if it is hard to estimate individual performance by inspection, how futile and hopeless appears the task of estimating transmitting abilities by inspection.

Individual selection can be practiced in terms of separate characters or in terms of general average excellence. In hogs we might decide to cull all animals with weak pasterns or those with steeply sloping rumps or those with heavy jowls. In doing so, we might be throwing away many genes for high fertility, for high proportion of valuable cuts, for large milking ability, etc. Likewise in keeping the good pasterns, rumps or light jowls, we might also be keeping low fertility, poor quality, lack of ability to raise pigs, etc. If selection were practiced on the basis of general average excellence, we would perhaps keep some sows with poor pasterns, steep rumps, and heavy jowls because they had enough other good qualities to give them an average score that was higher than other

sows which might excel in some specific characters. Similar illustrations can be envisioned in all classes of livestock. It is often noted with a beginning class in livestock judging that as specific animal faults are pointed out, each one in turn tends to bulk too large in the beginning student's mind, so that an otherwise excellent animal which exhibits this particular fault is dropped clear to the bottom of the class. Some students find it impossible to overcome this tendency. Improvement in livestock judging on the part of other students is merely the growth in ability to balance defects or imperfections and arrive at a sound judgment based on the total average excellence of the animals in each judging ring. The good judge sees all the good and the poor points of his animals but makes his placing on the basis of general balance of all parts. The good breeder practicing phenotypic selection does the same thing in his own "Little National or International" that he holds in his own barnyard.

The shortcomings of selection based on individuality can best be illustrated by calling to mind excellent individuals that have failed to transmit their own good qualities to their offspring. There have probably been many animals that stood at or near the top in the show ring and at the same time were mediocre or worse as breeders. Likewise, some animals that stood lower in their show classes, or perhaps were never deemed worthy of showing, have proved to be excellent transmitters of desirable type.

An instructive and helpful exercise is to lead out a group of animals and arrange them one behind the other in family groups according to their several generations as indicated in Fig. 158.

	Female lines			
Aged mares	A	B	C	D
Offspring by sire 1	..	B_1	C_1	D_1
Offspring by sire 2	A_2	B_2	..	D_2
Offspring by sire 3	A_3	B_3	C_3	D_3

FIG. 158.—Diagram of a breeder's show by families.

Reading down in Fig. 158, we have female lines, reading across we have male lines. It sometimes happens that the best mare, for instance, B, might have the poorest offspring and perhaps the poorest mare C the best. Not only can the best transmitting female lines be easily seen in this fashion, but the strong and weak points of the offspring of each succeeding male can easily be recognized and summarized. Exercises of this sort make it evident to the breeder which families should be perpetuated and which allowed to die out.

Pedigree and Selection.—After the individuality of the animal has received due consideration, it becomes necessary to consider carefully

the pedigree. A good individual that has back of it a poor pedigree should be tested thoroughly before being allowed to perform heavy breeding service. It is possible, of course, that this favorable "nick" will prove to be prepotent, but more likely that it will not. The only way to ascertain any animal's powers is to test it by means of its offspring. If we had to make a choice between a better individual whose ancestors were known to be poor and a poorer individual whose ancestors were known to be good, the wiser choice in terms of genetic worth would be the latter.

Unless the breeder can call up a mental picture of most of the animals represented in a pedigree for two or three generations back, and unless he knows intimately, through contact or study, the good and bad features embodied in these individuals, he is in no position to pass a reasonable, sensible judgment on the animal in question. Selection based primarily upon pedigree has in the past often failed of its purpose. Nevertheless, the best indicator of the type of offspring any animal is likely to produce is the type of ancestors found in the first two or three generations of its pedigree.

It should be recognized, however, that the ancestors of any given animal have themselves generally been highly selected, and the information about them is also of a highly selected character. This tends to raise our expectations too high, so that in general we can expect an animal to fall somewhere between the breed average and the average of its nearby ancestors.

A pedigree is, of course, merely the ancestors of an animal arranged in some logical order. Pedigrees are made possible through the purebred breed associations, which have registered animals and preserved records of lineage. These purebred breed associations have been of inestimable benefit in promoting the livestock industry. However, like other man-made institutions, they also have their faults. One of the greatest no doubt is the unselective nature of their work. All that has been necessary for the registration of an animal has been the requirement that its sire and dam were registered. This has inevitably led to the perpetuation of a considerable amount of germ plasm that the breeds would have been better off without. This makes the evaluation of pedigrees exceedingly difficult at times.

To be of any real value the pedigree must be complete, *i.e.*, in terms of records and accomplishments of the animals it contains, as well as a goodly portion of the collateral relations, and it must be interpreted scientifically. It is not yet possible to make pedigrees complete in this sense, and we are just beginning the attempt to interpret them scientifically, an attempt beset with many difficulties. Many fallacies have grown up about pedigrees. One of these consists in laying great store in the fact of the inclusion of some noteworthy animal many generations

back in the pedigree. We know, of course, that this in itself means nothing. Another shortcoming of pedigrees has resulted from the tendency to include only the advantageous material and to exclude the doubtful or harmful. If we are going to make progress in breeding, however, it is essential to know the whole truth as far as we can. The incompleteness of pedigrees is well-evidenced in Fig. 159.

Sire:
Brookmead's Frederick, 169802
"Royally bred young bull, tracing to some of the greatest animals bred at both Langwater and Pencoyd Farms."
Maternal brother to:
Langwater Stars and Stripes, 2d 44664AR
18 AR Daughters, 13 AR Sons
Brookmead's Royal Master of Riverview 50363AR
Sire of 7 AR Daughters

Langwater Master Fred, 51494AR
1st pr. get of sire, Bryn Mawr, Pa. and Far Hills Show, N. Y., 1932.
25 A.R. Daughters, 10 A.R. Sons
Brookmead's Veronica, AR14392
11014.9—625.78—Class G
13431.8—806.9—Class B
14502.5—864.6—Class AA
Brookmead's Patricia, AR26058
11363.6—674.8—Class F
12410.6—725.4—Class A
Brookmead's Hildafred, AR22009
10438.6—641.4—Class G
11982.2—712.0—Class C
Brookmead's Ideal Queen AR15951
11025.0—630.5—Class G

Quaker Girl of Pencoyd, 49194 AR6869
8898.00—457.6—Class B
3 AR Daughters, 2 AR Sons
Brookmead's Quaker Lady AR13405
13795.6—671.4—Class A
Brookmead's Water Lily AR16313
9967.4—517.8—Class G
Brookmead's Myrtle AR15419
9505.7—503.4—Class G

Dam:
Oaks Farm Emily, 292161

Aiyukpa Happy Lad, 136631
Sold for $1,000.
Full brother to:
Aiyukpa Happy Marmion 122784
1st pr. 2 yr. old (Breeders' Award 1)
Member 1st pr. graded herd, Eastern States, 1928. 2nd pr. 2 yr. old (Breeders' Award 2) National, 1929.

Oaks Farm Cammilla, 231500
"Was started on test and making a large record and was sold"

FIG. 159.—Pedigree of Oaks Farm Graceful, 344905.

Written up in this form, a pedigree may be made very interesting but it fails utterly in helping one to secure a worth-while and fairly

complete picture of the genetic make-up of the individual concerned. The sire in this pedigree is listed as being a maternal brother to some other bull, said other bull having some AR daughters, etc. Even though the sire were a full brother to the greatest bull that ever lived, nothing would thereby necessarily be proved as to his own worth.

The writer once made a study of 400 bulls in one of the dairy breeds which had been indexed on the basis of 10 or more daughter-dam comparisons based on Advanced Registry (selected) records. Of these bulls, 86 (group A in Table 42) had indexes of over 700 lb. of butterfat and averaging 756 lb.; 79 (group C) had indexes from 600 to 649 lb. and averaging 624; whereas 93 (group E) had indexes below 550 lb. and averaging 496 lb. Table 42 shows the values in terms of indexes of bulls and records of cows for amount of milk and butterfat test as they appeared in the pedigrees of these three groups of bulls.

TABLE 42.—AVERAGE OF RECORDS IN PEDIGREES OF BULLS IN GROUP A, C, AND E

	Group A	Group C	Group E
Sires (average index)	12,680—5.23	12,354—5.18	11,900—5.07
Dams (average record)	13,796—5.14	13,287—5.12	13,473—5.03
Paternal grandsires (average index)	12,435—5.12	12,312—5.10	11,964—5.10
Paternal granddams (average record)	14,092—5.11	13,467—5.12	12,962—5.10
Maternal grandsires (average index)	12,513—5.18	12,531—5.26	12,472—5.10
Maternal granddams (average record)	13,426—4.95	12,474—5.02	12,057—4.91
1st great grandsires (average index)	12,910—5.07	12,578—5.07	12,592—5.07
2d great grandsires (average index)	13,038—5.00	12,390—5.08	12,451—5.11
3d great grandsires (average index)	12,434—5.13	12,433—5.39	12,288—5.08
4th great grandsires (average index)	11,747—5.06	12,902—5.07	12,481—5.09
Average	12,907—5.10	12,673—5.14	12,464—5.07
Total Butterfat	658	651	632
Pedigree, percentage completeness*	60.2	53.3	44.2

* In terms of indexes on all bulls in pedigrees for three generations and records on all cows in pedigrees for two generations.

It is obvious that there was little or no difference in the records found in the pedigrees of the best and poorest transmitting bulls. The dams of the best bulls had records that averaged 13,796—5.14 per cent test; those of the poorest bulls 13,473—5.03 per cent test. The point of course is that pedigrees made up with selected records are valueless. It would be better from a breeding standpoint to have no information at all rather than selected or biased misinformation.

Hoard's Dairyman ran a bull-guessing contest in 1932. The bulls were pictured and their dam's records listed together with the record of their sire's dam, where available. Table 43 shows these records and the standing of the bulls in terms of their daughters' records.

TABLE 43.—BULLS' PEDIGREE RECORDS AND DAUGHTERS' RECORDS*

Bull	Dam's record, pounds fat	Sire's dam's record, pounds fat	Cows bred to average record, pounds fat	Bull's daughters average record, pounds fat	Difference between dams and daughters	Per cent of daughters excelling dams
E.	570	No record	472	526	54+	70
D.	581	570	419	483	64+	89
J.	559	No record	430	443	13+	57
A.	821	766	443	448	5+	50
B.	711	626	469	463	6−	41
G.	433	No record	478	439	39−	40
K.	No record	No record	465	419	46−	29
F.	525	570	448	397	51−	21
I.	620	711	476	385	91−	20
H.	841	736	484	318	166−	6
C.	589	527	428	225	203−	0

* *Hoard's Dairyman*, Oct. 25, 1932, by special permission of W. D. Hoard and Sons Company.

It is evident from the foregoing table that there was no correlation between the size of the dam's record and her sire's dam's record and the production of the bull's daughters.

This fallacy of attaching great significance to the record of the dam of a bull is further emphasized by the experience of one of the well-known Guernsey breeding establishments. They selected three bulls whose dams averaged 965 lb. of butterfat on a mature basis. These bulls were bred to better than average cows with the apparent expectation that the resulting daughters would average over 900 lb. of fat. The composite pedigree of these three bulls is shown in Fig. 160.*

The three bulls were bred to cows that averaged 533 lb. fat. The resulting daughters averaged 617 lb. fat

- Sires: Index, 662 lb. fat on 64% of their registered daughters, *i.e.*, all available daughter-dam comparisons
  - Grandsires: Index, 692 lb. on 54% of daughters
  - Granddams: Average record, 681 lb.
- Dams: Average record, 965 lb.
  - Grandsires: Index, 550 lb. on 33% of daughters
  - Granddams: One record, 631 lb. Other two had no records

FIG. 160.—Composite pedigree of three Guernsey bulls.

* The index here used is the Intermediate. Indexes are discussed fully in the next chapter.

It is well-known that the record of a cow is not necessarily an indication of her genetic make-up. Even if it were, why should one expect that the granddaughters of these high-record cows (daughters of their sons) would receive the bulk of their inheritance from their paternal granddam. There are three other animals in this second generation, besides the two parents, which actually contributed the germ cells with their genes or determiners of potentialities. If we use the material in this composite pedigree, sketchy though it is, in an intelligent manner, we can get a fair estimate of the breeding worth of these three bulls. Let's average the figures shown for the two parents and take 0.6 of it, for this is the first generation. Then average the figures shown for the second generation and take 0.4 of that in order to get unity or 1. When this is done, we get a figure of 743 lb. Now these bulls were bred to cows that averaged 533 lb. of fat, and, if the sire and dam contribute equally to their daughters, these resulting daughters should have averaged about halfway between 743 and 533, or 638 lb. of fat. They actually averaged 617 lb. of fat.

The fact that certain outstanding animals have been the result of the mating of animals related in some certain way has led some breeders into the grievous error of assuming that there is something in the system of mating or breeding that leads to the beneficial result. This, of course, is pure fallacy and in the same category as heading the cow to the east during service to secure bull calves and to the west to secure heifer calves, etc. The fact that the bull Favorite was bred back to his own dam and the heifer that resulted bred back to her own sire Favorite to produce the famous Shorthorn bull Comet has not necessarily the remotest connection or significance in any Shorthorn herd of today. True, this system of matings was successful in this instance, but that does not prove that it would ever be successful in any other herd at any other time, and it may have been pure chance that made it successful in producing Comet. Anyone who tries to breed animals according to some preconceived formula may, of course, succeed but if he does it will be due to the make-up of the germ cells and fortuitous combination of genes, not to the system followed. Yet we have all sorts of breeding formulas proposed, *e.g.*, (1) mate a maternal (or paternal) half brother and sister; (2) mate a cow with a son of a full sister; (3) mate a bull with his maternal (or paternal) granddam; (4) mate a bull to his granddaughters; (5) mate a grandson of a great bull to a daughter of another son of the great bull, etc., ad infinitum. There is little or no likelihood of one's making any significant success in attempting to breed animals according to some pedigree formula.

Unjustified merit is sometimes assigned to any and all animals of certain strains or families. In common vernacular, this is known as a

"pedigree craze." They are sometimes propagated for the sake of restricting competition, and the livestock breeder will do well to investigate thoroughly before shaping his course by them. Utility rather than popularity will, in the final analysis, be the criterion by which all classes, breeds, strains, and individuals will be tried. This should not be construed in any way to mean that certain strains or families are not better producers of speed, milk, flesh, wool, or what not, than are others because such an interpretation would be entirely removed from the truth.

In planning matings, pedigree study has a legitimate place. Hard and fast rules cannot be laid down. It is a matter of reflection and judgment requiring intimate knowledge of the dominant characteristics of the strains in question. Some strains are too fine, others too coarse, some mature quickly, others slowly, butterfat percentage is high in some, low in others. To mate wisely, so that in all probability there will be blended in the offspring some of the extremes found in the parents is an art in the achieving of which pedigree study has its legitimate function.

It will readily be recognized that the number of animals in the most efficient strains is more or less limited. It is also a fact that because of their recognized merit there is a large demand for them, and they consequently sell for high prices. To the small breeder, this is discouraging, but he need not be without hope. These, to be sure, are proved strains, though, when their origin is studied, it is found that they arose more or less by chance through the mating of two particular individuals. Each parent probably supplied some previously missing factor or factors, which when combined into one individual yielded an animal of much greater worth than either parent and, moreover, an animal capable of transmitting its own good qualities. It would be foolish to believe that what has occurred cannot be repeated. The small breeder with limited capital may, through a proper blending of strains, produce a strain more beautiful and more efficient than anything yet known. This does not mean that any breeder can be careless in selecting foundation stock or, in general, expect to get something from nothing. He should, by all means, select from proved strains as far as his finances will allow, because the isolation interpretation explains nuch more logically than does the mass-selection interpretation the progress that has been made in the past. When an outstandingly good animal arises from mating two more or less mediocre animals, the progeny-performance test must be very rigidly applied.

Gowen has studied the A.R.S.O. records in the Holstein-Friesian breed in order to find answers to the following questions: (1) Is the milk yield of a cow determined by her sire either in whole or in part? (2) Is the milk yield of a cow determined by her dam either in whole or in part? (3) Do the grandparents or ancestors further removed have any marked influence on the milk yield of their granddaughters? He secured the

following correlation coefficients: coefficients of milk yields of full sisters 0.55; half sisters with the sire as the common parent 0.37; half sisters where the dam is the common parent 0.38. From these figures he concludes that the joint influence of sire and dam makes for greater resemblances between two sisters than for either of the half sisters and that the influence of the sire or dam on milk yield of half sisters is approximately equal. The correlation coefficients between granddaughters' milk yields for the paternal grandsire was found to be 0.07 and the maternal grandsire 0.24, indicating that the grandsires influenced the milk yield of their granddaughters to about one-half the extent of the parental influence. The correlation coefficient between milk yields of daughters and dam was 0.50, between granddaughter and paternal granddam 0.26, between granddaughter and maternal granddam 0.31, indicating that the influence of each granddam is about equal and each about one-half that of the dam. This shows the influence of the grandparents to be about one-half that of the parents, and Gowen found that great grandparents show little direct influence on the milk yield of their great granddaughters.

Similar relationships to those given for the milk yield exist for the butterfat percentage. The correlation coefficient for the butterfat percentages of full sisters is 0.52; that for the half sisters where the sire is the common parent is 0.38; that for the half sisters where the dam is the common parent is 0.12. The correlation coefficients for the granddaughters of the paternal and maternal grandsires are 0.18 and 0.22, respectively. The direct relationship of the butterfat percentages of daughter and dam is 0.41. The correlation coefficients for the granddaughters' butterfat percentages with the paternal and maternal grandams' butterfat percentages are 0.09 and 0.19, respectively. These constants make it clear that the same general relationships exist for the inheritance of butterfat percentage as exist for milk yield. In other words, the bull and the cow are jointly and equally responsible for the milk yields and butter fat percentages of their daughters. The grandparents influence the milk yields and butterfat percentage of their granddaughters to only about one-half the extent that the parents affect these variables.

A basis is now established for a consideration of certain practices in use in animal breeding. It is obvious that only those ancestors in the first and second generations are of any pronounced influence on the milk yields of their progeny. Such being the case, it is equally clear that much of our pedigree study as it has been carried on in the past is faulty, since the greatest emphasis is laid on those animals occurring in the third and fourth generations of the pedigree. Instead of trusting to famous ancestors in the third or fourth generation, let us insist rather that the parents have high milk records.[1]

[1] Gowen, J. W., The Inheritance of Milk Yield, etc., *Amer. Soc. Anim. Prod. Proc.*, 1922, p. 103.

The greatest lack in animal breeding today is the lack of records. Until this deficiency is remedied, pedigrees will continue to be of relatively little use in enhancing the accuracy of selection. Attempts at remedying this situation are being made by some of the purebred breed associations by means of records of performance, but the problem is a very difficult one and a complete solution is not to be expected immediately.

Any individual breeder, however, is at liberty to set up his own system of record keeping at once, which greatly enhances his chance of successful selection in his own herd. Such systems of record keeping will be indicated for each of the classes of livestock in the next three chapters. Even when pedigrees can be made relatively complete from the standpoint of records, we must realize that we can probably never have a complete knowledge of the genetic make-up of any animal, and, even if we did, we would still have to face the sampling nature of the hereditary process, which would make it uncertain which member of each heterozygous pair of genes any individual actually received from its parents. Whether we gain more than we lose by culling a certain fairly good individual because of some fault in its pedigree is an unanswerable question. Again, as was said of judging or estimating individuality, we must try to strike a proper balance between individuality and pedigree.

The breeder's first concern will be to select good individuals. Complete pedigrees in terms of records of performance would be of inestimable benefit to him in deciding to keep one or another of two individuals of approximately equal merit. Complete pedigrees can be of great benefit also in arriving at an estimate of different female lines within a breeder's own herd. When pedigrees can be made relatively complete in terms of records of performance, one will also have considerable data on the collateral relatives of each individual, and, although it is difficult or impossible to assign definite numerical values to records of collateral relatives, they will, nevertheless, be very valuable in a general way.

Progeny Test and Selection.—The idea of progeny testing as an aid in selection has lately been revived and given much publicity. Like many other general ideas, this one is not new having been advocated by the Roman, Varro, 2,000 years ago and having been used by Robert Bakewell in the eighteenth century in his practice of bull and ram letting. The progeny test finds its greatest usefulness with characteristics that can be expressed by only one sex, *e.g.*, milk or egg production, although there is no reason why it cannot be used to advantage with any class of livestock. Like any other selection device, this one has both advantages and disadvantages.

Owing to the relatively few offspring of most females, it cannot in general be applied to animals of this sex. Even with males their progeny-performance rating must come relatively late in their lives, after a suffi-

cient number of their offspring have been born and reached such an age that their own performance has had time to be measured. Care must be exercised that excellences or deficiencies which are actually environmentally caused be not ascribed to inheritance in either the offspring or the parents. Allowance must be made for the fact that the females to which a male is bred are generally a somewhat selected group. It can thus happen that a breeder can be making progress even though the total offspring of each of a series of males averages lower than their dams. We must not forget that the hereditary process is of a sampling nature, and we therefore will need enough comparisons to make reasonably sure that we have a fair sample of any male's inheritance.

Even with the above limitations, progeny testing is one of the keenest tools available to the breeder. It should be used to supplement individual and pedigree selection—not to totally displace them, as is sometimes advocated. The simplest type of progeny testing consists of the average record or merit of a sire's offspring. If the females to which two males are bred are an average of the breed as a whole, then such progeny records can be used to measure the breeding value of the two males concerned. If, however, the mates of one male were considerably above breed average, those of the other considerably below it, then such comparisons would not be justified.

Among the farm mammals, progeny testing has been used most with dairy cattle, a little with swine, and is just beginning to be used with the other classes. In dairy cattle, progeny testing has eventuated in several systems of indexing bulls for their level of transmitting ability for amount of milk and butterfat percentage. The system generally used can be illustrated by the following example. Suppose a bull is bred to 12 cows whose average production is 7,000 lb. of 3.8 per cent milk, and their daughters by this sire average 9,000 lb. of 4.0 per cent milk. Presumably this bull has raised the production of his daughters by 2,000 lb. of milk and 0.2 per cent of butterfat. Because these qualities are apparently controlled by multiple genes, we assume that the sire and dam are jointly and equally responsible for the production of their daughters, in other words, that the daughters' production falls halfway between the two parental levels. Knowing the level of production of the cows and their daughters enables us to estimate the transmitting level of the bull.

	Pounds	Butterfat percentage
Dam's production	7,000	3.8
Daughter's production	9,000	4.0
Bull's index	11,000	4.2

It is obvious that before such figuring is justified the records of both dams and daughters must be corrected to some standard basis. This is accomplished by means of various and sundry conversion factors. It is tacitly assumed that if the bull were sold to another breeder whose herd production also averaged 7,000 lb. of 3.8 per cent milk the resulting daughters would also average 9,000 lb. of 4.0 per cent milk. This might or might not be the case, depending on many things, but especially on *the genetic make-up of the animals involved. Many different gene* combinations might conceivably result in a production of 7,000 lb. of 3.8 per cent milk. Whether this proved bull would nick equally well, better, or worse in the second herd could only be ascertained by trying.

The U.S. Department of Agriculture Bureau of Dairy Industry proves bulls on the basis of 5 daughter-dam comparisons. Some investigators urge at least 6 comparisons, others 8 or 10. Obviously the error will be cut down as more daughter-dam comparisons are added, because the extreme variates will have a tendency to cancel each other thus giving a truer average. If a breeder can successfully standardize his records—smooth out the environmental differences—and will test the first 6, 8, or 10 daughters as they are born in his herd without any selection—he will get about as good a genetic picture of his bull as he would with 30 or 40 daughters.

Attempts are now being made to work out comparable and practical systems of indexing males in the other classes of farm livestock. When available, such information should aid greatly in taking some of the "guess" out of breeding. And, even though most males cannot practically be indexed until after they are dead, the information can appear in pedigrees, which makes them of much greater value.

Probably the greatest advantage to the breeder from progeny testing will arise from the records themselves rather than from their manipulation as indexes. When records are kept and intelligently studied, selection is bound to be benefited. Breeders too often depend on a somewhat unreliable memory and are prone to have favorites among their animals. Even a condemnatory record as a breeding animal at times fails to outweigh a breeder's fancy for some particular pet. Actually, of course, if one is not going to use the records, he is simply wasting his time in getting them. Progeny testing must be based on records, which, if carefully compiled and intelligently and, on occasion, ruthlessly used, can be the surest guide that a breeder can have.

Phenotypic vs. Genotypic Selection.—There are two possible interpretations of improved performance: (1) that selection in itself modifies the germinal elements and that by selecting in a specific direction the hereditary material itself is actually molded in a corresponding fashion and (2) that the effectiveness of selection depends upon the isolation of

hereditary material of the most excellent sort. It will be seen that the two views are diametrically opposed to each other, and it is necessary to make a choice of one or the other interpretation. Upon that choice will depend the method of selection adopted. If the first explanation is accepted, it will involve only mass selection of those individuals which are themselves better than average producers.

Mass or phenotypic selection was practiced with poultry at the Maine Agricultural Experiment Station beginning in the year 1899. From this time until 1907, only those females were used as breeders that produced at least 160 eggs in their first year, only males whose mothers laid at least 200 eggs in their first year. Under this system of selection, the yearly egg production decreased steadily. The point to be noted here is that mass selection failed to increase production in the hereditary material involved.

After 1907, the system of selection was changed. All females were now selected from high-producing mothers, the female progeny of which were all high producers and, in case such a female failed to yield high-producing progeny the first year, she was not retained in the breeding flock. Males were selected from high-producing mothers whose female progeny were all high producers, and a male was discarded immediately if his progeny failed to be high producers. Pedigrees were also kept and proper attention given to the blending of blood lines. With such a system in vogue, the production increased steadily from 1908 to 1920.

Here is critical evidence to substantiate the impotency of mass selection alone and the efficacy of individual selection plus progeny-performance test and proper blending of blood lines. In any breed of livestock, it is possible to show that improvement has come not through the gradual raising of production by the mass but through the blending either by chance or under man's guidance of a favorable type of germ plasm in one or a few individuals, which have, in turn, passed this favorable germ plasm on to their offspring. In Standardbred horses, the influence of Hambletonian 10 is as great as it is well-known. This animal, though not particularly fast himself, carried and passed to his offspring germ plasm with maximum possibilities for the development of speed. As Davenport has shown, the 10 greatest producers of speed in the Standardbred horse are all sons, grandsons, or great grandsons of Hambletonian 10. In Herefords, almost as great an influence has been wielded by Anxiety 4th, a strongly inbred bull.

Production, Type, and Show Ring in Selection.—Production is generally thought to be closely associated with type, which in turn is determined by the market as well as by show-ring standards. With meat animals, type is measured by the relative proportions between hams, legs, rounds, loins, ribs, bellies, and shoulders as well as their

proportion to the less valuable portions of the carcass. Type, in other words, in these classes is production, and to a certain degree it is evident to the eye before slaughter and is evidenced by both sexes. In horses, certain types of build have been found by experience to be better suited for certain performances than are others, although temperament is also of great importance. In dairy cattle, there is somewhat less correspondence between external appearance and production, for the latter is due largely to the physiological functioning and coordination of organs and glands located internally.

An investigation by Gowen of the Maine Agricultural Experiment Station is of interest in this regard. The following figure (161) shows the relative efficiency of even short records as indicators of yearly production

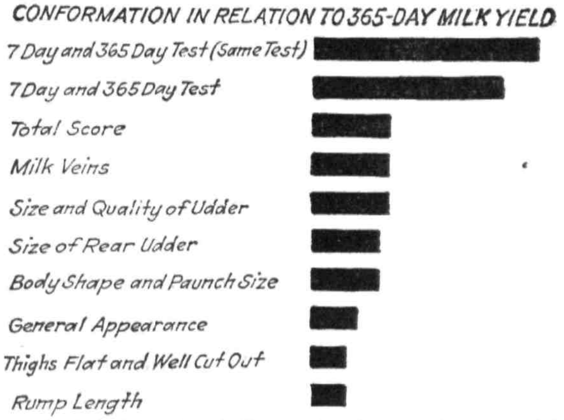

FIG. 161.—The length of the black bars indicates the relative value of the different points as measures of milk-producing capacity. (*After Gowen.*)

as compared with the total score of the animal and the score in several respects commonly believed to be indicators of productive capacity.

Pausing to consider briefly these facts we see that a seven-day test might be considered as an objective test, whereas the value of the points of conformation are a subjective test for the cow's producing ability. That is, the seven-day test is simply dependent on the reading of the scales that weigh the milk, whereas the use of a scale of points to judge a cow for milk yield depends, not on any external scale, but on the mental processes or mental ability of the judge so to balance his cuts as to show the true worth of the cow. From this it follows that the conformation of the cow as a measure of milk yield would in all probability be subject to the personal bias of the judge.

This is, in fact, shown to be the case in study of the records. There are nineteen men, all well-trained dairymen, who have judged enough cattle with milk yield to make a test of their ability as judges of these cows for milk yield., Nine of these men clearly could judge dairy cattle by the score card and select

the better milkers. On a scale ranging from 1 to 0 and 0 to −1 (correlation scale) these men varied from the most accurate judge of milk yield from the conformation of 0.614 to the least accurate judge of −0.098. The average ability of these men is 0.246, or they are, on the average, about 25 per cent better judges of dairy cattle for milk production than the average trained dairymen. Clearly, some men are good cattle judges. Equally clearly, some men cannot judge cattle for milk production by the use of the score card. Such being the case, the individual man will do well before he selects cattle by their conformation alone to make a sufficient test to convince himself that he is one of those gifted men who can judge dairy cattle.

On the other hand, almost anyone can weigh milk. No personal equation need be present in recording the weights. Such being the case, when they are obtainable the dairyman or buyer would do well to consider the milk yield carefully in selecting dairy cows as indicated by the figures above.[1]

Both the Jersey and Holstein breeds of dairy cattle operate voluntary systems of classifying animals according to type, and most of the animals classified do have production records. Table 44 shows the production records of all Jerseys classified for type up to Mar. 31, 1939.

TABLE 44.—PRODUCTION RECORDS OF ALL ANIMALS CLASSIFIED TO MARCH 31, 1939

Classification groups	Number of cows classified	Number of cows with R. of M. or H.I.R. records	Percentage of cows with records	Average mature production of each group
Excellent	344	280	81.40	655.42
Very good	1,243	869	69.91	619.78
Good plus	2,307	1,416	61.38	595.64
Good	1,598	821	51.38	576.89
Fair	232	103	44.40	573.50
Poor	15	1	6.67	557.00
Totals	5,739	3,490	60.81	601.48

The annual report of the Jersey breed for 1939 says in discussing this table:

A careful examination . . . shows a definite correlation between the type classifications and the production records of the cows. This is particularly true for the cows classified last year and indicates that with experience, the ratings given by the classification judges are now showing more correlation with production than was formerly the case. The increases in production are significant, particularly when it is observed that a larger percentage of the higher rating animals have been tested for production than is the case with the lower rating

[1] GOWEN, J. W., Report of Progress on Animal Husbandry Investigation, *Maine Agr. Expt. Sta. Bul.* **299**, pp. 87–88, 1921.

animals. Undoubtedly if an equal percentage of each classification group had been tested, the differences in production would be much greater.

The table does indicate that there is definitely some relationship between the conformation of a cow and her producing ability and that both good conformation and high production can readily be combined in the same animal. They are certainly not inimical to each other. On the other hand, Herd Classification is not intended to supplant production testing. It seems a fallacy to suppose that by breeding solely for production, we may secure ideal breed type or that by breeding with type alone in mind, we can secure the ideals in production. Jersey breeders must continue to select and breed with both ideals in mind and only by following such a practice can the Jersey cow be definitely improved and a higher standard reached in conformation and producing ability.

In the writer's opinion the word *correspondence* might better have been used in the above rather than the word correlation. Undoubtedly there is some positive correlation, but it probably is low. A low correlation simply means that one would have a somewhat better chance of getting good production by selecting good type animals from this population than if he just selected from them at random. But it would also be true that many good type animals would not be among the highest producers and that many high producers would be found among those which did not classify in the highest brackets.

Correlation studies between type and production in classes of livestock other than dairy cattle have not been numerous. As would be expected, a fairly high correlation has been shown between weight and draft power in horses. In meat animals, type presumably is production, though many factors are concerned in the question as to whether the best type animal will net the feeder the greatest profit, among the most important of which are the initial cost, the rate of gain, and the efficiency of feed conversion. That there are considerable differences among animals in their ability to convert feed into flesh is well-known, but there seems to be no evidence that this is associated with any specific type characteristics.

The show ring has undoubtedly had a major place in shaping the type of all the classes of livestock. The first American show was held at Pittsfield, Mass., in 1810, and since that time many thousands of animals have passed before the judges' eyes. As now constituted, our livestock shows have both advantages and disadvantages from the standpoint of breed improvement.

Among the latter are the following: (1) a possible lack of high correlation between showyard winning and efficiency of lifetime production; (2) a lack of opportunity to measure the transmitting abilities of the winning animals except in a very limited manner through the "get of sire" and "produce of dam" classes; (3) the fact that "fitting" for the

condition by laying on great stores of fat (which often results in temporary or permanent sterility) removing a goodly portion of the wool in blocking, etc.; (4) the practice of remedying defects by surgical means; (5) the keeping of animals from productive work or from reproduction in order to enhance their likelihood of winning in the show ring; (6) the fact that clever fitting and showmanship can cover up weaknesses of various sorts; (7) the fact that commercialized show herds making a circuit of shows tends to discourage or prevent smaller local breeders from showing; (8) the fact that the offspring of top show winners are apt to be sought as sires more or less regardless of their own or their winning parents' actual genetic merit.

Yet, in spite of these limitations, the show ring is the best medium yet discovered for molding breed type. This is probably its greatest advantage, but it has others, among them: (1) It brings breeders together for exchange of ideas and experiences; (2) it serves as the best advertising medium for both the breed and the individual breeder; (3) in a limited way at least it helps in discovering and popularizing the better genetic materials in the various breeds.

The show ring would be of greater service as an adjunct to breeding and selection (1) if it did not demand overfitting; (2) if the judges in all cases gave orally their reasons for their placings; (3) if in the classes of meat animals the animals could be slaughtered for carcass and cutout values; (4) if in horses a pulling and behavior test could be invoked, although it is realized that we want a steady all-day tractive exertion of 150 lb. rather than one of 1,500 lb. for 1 or 2 minutes; (5) if more weight could be given to the older breeding animals' actual accomplishments as breeding animals; (6) if in dairy cattle a satisfactory combination based on both type and production could be utilized.[1] This system of judging dairy cattle on a combined type and production basis is being used successfully at some fairs in the New England states.

In general, the livestock producer is interested in the type of animal that will make him the most money. Whether this is the type that is currently winning top honors at our livestock shows needs investigation. Since the show does wield such a great influence on type in the breeder's mind, and since the breeder is interested primarily in profitable lifetime production, these two angles need constant scrutinizing and for the best interests of all concerned should be brought and kept in line.

Sometimes men waste time and effort in selecting for some mark that is supposed to be positively correlated with productivity. The best example of this was perhaps the old escutcheon theory, through which some men thought they could foretell the milk yield of dairy cattle by means of the hair pattern found on the rear and inside of the thighs.

[1] Such a proposal has been formulated by W. W. Swett and R. R. Graves of the Bureau of Dairy Industry and is published as *U.S. Dept. Agr. Misc. Pub.* 409.

It has never been possible to prove the slightest connection between these two things, which in the light of common sense is not surprising. Some men think that a slight hump in the middle of a cow's back or a notch at the tail setting or heavy shoulder, etc., are correlated with high production. Selection based on all such things as these is missing the mark by a very wide margin.

Fertility and Health in Selection.—Earlier chapters of this book were devoted to fertility and sterility. Since, with most classes of livestock, usefulness and profitableness depend so largely on the number as well as quality of offspring produced, this is a matter that should receive a breeder's close attention in selection. In the purchase of mature breeding animals, one should ascertain their actual breeding history. If this is questionable or deficient, one would in general be much better off not to buy. In the purchase of mature males, semen tests will reveal the likelihood of fertility, though they cannot guarantee it in any special instance.

In the purchase of young animals with no breeding history, one must rely on the performance in this regard of its close ancestors and collateral relatives. Rate of fertility is, in the final analysis, controlled by the genes working through the endocrine glands and the genitalia and, of course, is greatly influenced by environmental conditions. No one cares for twin foals, few for twin calves. In sheep a certain proportion of twins are desirable, and in swine we want moderately good-sized litters. One should select, therefore, in a naturally fertile strain but avoid extremes. The size of the immediate litter in which a boar may have been born is of minor consequence, the fertility of the strain or family of great importance. Males in the other classes of livestock should be selected from fertile families and from dams that were regular breeders throughout their lifetime.

Much work has been done in plants in breeding up disease-resistant strains. In animals, there is little comparable to this as yet but there is evidence that some strains of animals are more resistant to certain diseases and other troubles than are others, and in some instances at least this appears to have a definite genetic basis. Card and Roberts have reported experimental evidence that seems to prove that "resistance and susceptibility to infection by *Salmonella pullorum* (in poultry) are due, at least in part, to the existence of dominant hereditary factors." Lambert, Speelman, and Osborn[1] have reported considerable differences

[1] Lambert, W. V., Speelman, S. R., and Osborn, E. B., Differences in Incidence of Encephalomyelitis in Horses, *Jour. Hered.*, **30** (8): 349–352, 1939.

See also Webster, L. T., Heredity in Infectious Disease, *Jour. Hered.*, **30** (9): 365–370, 1939.

Gowen, J. W., Contributions of Genetics to Understanding of Animal Disease, *Jour. Hered.*, **28** (7): 233–240, 1937.

in resistance to encephalomyelitis among different breeds of horses at the U.S. Range Livestock Experiment Station at Miles City, Mont.

In nature, disease susceptibility tends to be self-limiting, for the weak strains are not apt to leave as numerous a progeny as are the more resistant strains. In man this weeding out of the unfit and their bad genes is interfered with through hospitalization and the marvelous accomplishments of the medical profession. We are making beginnings along this line in our animals by means of vaccines and other preventives. Whether or not this is a wiser scheme than breeding and selecting animals with a natural immunity because of their genetic make-up the future must determine. Some diseases have no doubt been conquered by genetic means; others, like bovine tuberculosis, we have practically conquered by destroying animals that reacted to the test; others, like hog cholera, we have learned to live with through the help of vaccines. Human and animal diseases must be conquered if man is to persist on this planet, and perhaps there is no one best method for use in all cases. Since it is difficult if not impossible to make money from diseased animals, the intelligent breeder should use all the means at his disposal for securing naturally fertile, healthy, vigorous, and resistant animals and avoid at any cost the introduction of disease itself or susceptibility to any disease into his herd or flock.

In this category also, we might call attention to certain known lethals in livestock such as "bulldog" calves, cleft palate in pigs, skeletal defects in lambs and closed colon in foals. These abnormalities are due to specific genes. In selection, some attention should be paid to them and every effort made to avoid their introduction into a herd or flock.

Although in no sense a disease, such characteristics as red calves in Holsteins or Angus, bay color in Percherons, too light a red in Durocs, black skin spots in Chester Whites, etc., are from the purebred standpoint undesirable and should be guarded against by means of records and pedigrees as much as possible, although such things are often fairly successfully covered up. The same may be said for any character that detracts from an animal's quality as a member of a certain breed. Although many of these things are inconsequential from a utilitarian standpoint, they are of consequence from the standpoint of the pure breed. Only fertile, healthy, vigorous animals that are typical of their breed in all respects should be admitted to one's own group of purebreds.

Averages and Selection.—Since the environment may play such an important role in the actual productivity of any animal, it is important that the breeder give the matter some attention in making his selection of breeding animals. In dairy cattle, for instance, age, length of time pregnant, season of freshening, number of times milked, general health through the lactation period, etc., may have very important bearings on

the actual amount of milk a cow produces in any given lactation. In order to compensate for these environmental influences, correction factors have been devised. The only two that are widely used are those for age at freshening and number of days or number of times milked. From the standpoint of genetics or breeding, the only differences with which the breeder is concerned are those having a genetic basis. He must attempt, therefore, to smooth out the environmental differences by correction factors or otherwise in order to make the performance of his animals comparable. Similarly, the growth rates of beef calves, the number of

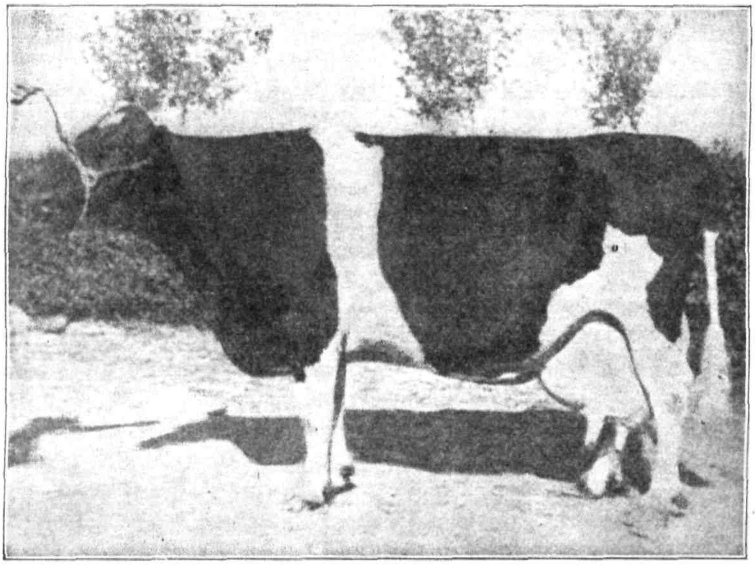

FIG. 162.—Adirondac Wietske Dairy Maid, a Holstein cow with four records each above 30,000 lb. of milk and 1,000 lb. of fat.

pigs that a sow bears and raises, the amount and quality of wool produced by sheep may be greatly influenced by the environment.

One of the best and easiest ways of compensating for these environmental influences is through the use of production averages. A cow might make 500 lb. of fat one year, 600 another, and 400 another. It is likely that her level of inheritance for butterfat production is nearer to the 500-lb. level than to the 600- or 400-lb. levels. In all qualities that are variable and that may be expressed on more than one occasion, an average of several measurements will prove safer and more accurate than any one measuring. With several opportunities to express a certain quality, the high and the low expressions are likely to cancel each other, though they will not necessarily do this. For safety's sake, therefore, the average of many records of production or measurement should always

be applied to breeding animals in order, in so far as possible, to eliminate the influence of extremely bad environmental conditions. Along with the records that every breeder should keep must go the ability to judge and evaluate *fairly* a host of environmental conditions which play upon the lives and producing capacities of his animals. Only with this technique or art well-developed will the breeder be able to arrive at the point where he can evaluate actual genetic differences on which, of course, the entire success of his effort as a livestock breeder depends.

Balance and Selection.—We have already discussed a number of general items that should be borne in mind in selecting breeding animals, although we have by no means exhausted the list. Additional items will be presented in the three following chapters as they apply specifically to certain classes of farm mammals. One further matter of a general nature should be mentioned at this point, *viz.*, that of always keeping in mind a general balance sheet between all the items which it may be the purpose of the breeder to attempt to incorporate into the genetic pool of his own herd or flock. It is generally very easy to be a radical, to go to extremes, and very difficult to stick to the middle of the road or to find the happy medium.

For example, in selecting the breeding animals, it would be easy to go to extremes in draft horses and attain great weight and power at the expense of movability; or, in fast horses, to attain great speed at the expense of such a high-strung nervous organization as to make performance either in racing or reproducing difficult of attainment; in dairy cattle, to attain tremendous producing powers at the expense of regularity of reproduction over a long lifetime; in meat animals, to attain great ability to fatten at the expense of reproduction or conversely to attain great reproductive powers (twins in cattle, triplets or quadruplets in sheep, litters of 20 or 25 young in hogs) at the expense of vigor and general ability to yield a desirable carcass in a short period of time.

The good judge of livestock is a man who is able to balance successfully the defects of one animal against those of another. Likewise the good livestock breeder is the one whose selection yields him a proper balance in his animals of all the various and sundry qualities they must possess if they are going to be profitable.

We all realize that it would be very much more simple to select for only one quality at a time and, when we had that thoroughly incorporated into our herd or flock, to start on the next item. The drawback to such a scheme is the fact that, while we are getting the one desirable quality we want established in our herd or flock, we may also be getting one or several very undesirable things established also, provided we are practicing no selection against them. For example, we might select for nothing but high milk production in dairy cattle, and we could undoubtedly

secure it, but, if it came at the expense of badly pendulous and broken away udders or lack of general vigor, disease resistance, or longevity, it might not be worth the price. Or we might practice selection for a 4 per cent butterfat test in Holsteins to the exclusion of all else. Again we could undoubtedly be successful in this aim, but, if we got it at the expense of a greatly lowered total amount of milk, it probably would not be worth this price.

From a practical standpoint, therefore, we must reconcile ourselves to the task of generally selecting *for* several things and also selecting *against* several things at the same time and trying in general to strike a happy medium, a balance, between the best and the worst in several respects.

Summary.—We have seen in this chapter that intelligent selection of breeding animals presents a great variety of problems. The main purpose of selection is to increase our stock of desirable genes and to diminish our stock of undesirable ones. Since we cannot examine the genes themselves, our only recourse is to estimate them by studying individuality, pedigree, and progeny. In addition to the difficulty of not being able to read the labels on the genes directly, there are the further complications due to dominance, epistasis, and probably other unknown interactions between the genes as well as those caused by the environment. To be effective, our selection must be on the basis of variation caused by genes, since environmental variations so far as known are in no sense hereditary.

The breeder must first study his probable market and produce what the market is anxious to buy. He must then select the breed of animals that will best fulfill his own peculiar market demands. His individual selections must be guided by individuality, pedigree, and progeny performance. He must select for the type of animal that will most efficiently serve the production needs of his market over a long life of usefulness, a type set, it is to be hoped, by the show ring. He must above all else select fertile, healthy, vigorous individuals from strains or families of similar qualities, and he must base his selection on high average lifetime production rather than on the basis of single, exceptional performances. Selection, the key to animal breeding, is a many-sided problem. To weigh properly all the factors involved is far from easy, but on the success of such weighings a breeder's ultimate success depends as on no other one consideration.

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CHAPTER XXIII

SELECTION IN DAIRY CATTLE

Dairy cattle are found on about 75 to 80 per cent of the farms in the United States, and their products account for about 20 per cent of the total farm income. Of the 25 million dairy cattle in the United States, only about 5 per cent are purebred and registered, the remainder being 80 per cent grades and 15 per cent nondescripts. The average production of all dairy cattle is estimated to be about 4,600 lb. of milk a year. Dairying is thus seen to be one of the most important phases of animal husbandry and one greatly in need of improvement as far as the machinery of production, the individual cow, is concerned. Dairying is of special importance near the large centers of population.

In one respect, selection of dairy cattle is somewhat easier than with other classes of farm mammals, for a measure of a cow's producing ability in terms of milk and butterfat may be secured over her whole productive life. We can thus have tangible evidence of her average yearly or lactation yield as well as that of her female offspring, though such actual records are available on only 5 to 7 per cent of our dairy animals. In another respect, dairy-cattle selection is more difficult than in other livestock classes, since, if actual records are not available, it is difficult if not impossible to estimate from the exterior form what the internal functioning will yield in terms of milk and butterfat. In this class of livestock, too, the male shows no evidence of the quality for which the species is kept; *i.e.*, the bull yields no milk, so that his genetic quality can only be measured by the roundabout method of comparing the production of his offspring and his mates. Selection is further complicated in dairy cattle by the fact that breeders desire their animals to evidence the approved dairy type in addition to being high and profitable producers, and the two things are not necessarily closely correlated.

In spite of the difficulties, enormous progress has been made in improving both the type and the productiveness of our dairy animals. We have no pictures of the general type of cow that our savage, cave-dwelling, or nomadic ancestors tended, but it seems probable that it would win nothing but derision or a laugh if led into a modern show ring. The earliest cows produced enough milk to help nourish their calves for 1, 2, or 3 months, a few hundred pounds at the outside, whereas many thousands of Dairy Herd Improvement Association cows average over 8,000 lb. of

milk yearly, and the record production by a single cow stands close to 42,000 lb. of milk in a year. Progress has been made, and breeders have made it for the most part with the presently considered clumsy tool of a belief in the old adage that "like begets like" or phenotypic selection. Most breeders still find this tool useful, but it can be sharpened considerably by considering records of performance on the part of collaterals as well as ancestors and progeny.

A hunt for superior germ plasm in dairy cattle was instituted by the Bureau of Dairy Industry in 1936. In all a total of 1,097 herds of dairy cattle that had continuous records for a long enough period to have proved at least two sires on the basis of comparing their daughters' and their mates' records were surveyed. Of these, 708 herds located in 40 states and including seven breeds had complete enough data to be included in the summary, of which 157 herds were deemed to have made progress, the other 551 not. The 17 foundation cows, which was the average number, in the 157 herds averaged 447 lb. of fat; the 62 average additions to these herds averaged 498 lb., giving a cumulative average of 487 lb. of butterfat. The remaining 551 herds had an average of 15 foundation cows with records averaging 433 lb. of fat; the 40 additions averaged 431 lb. of fat with a cumulative average of 431 lb. A total of 4,309 sires were used in the 708 herds, and 2,242 of them could be proved through five or more daughter-dam comparisons. About 32 per cent of these bulls raised production of their daughters over their dams; 20 per cent held it; and 48 per cent lowered it. The average herd reported on six sires, which left a total of 39 daughters whose production was 451 lb. of butterfat while their dams had averaged 452 lb. A few herds had made fairly steady progress, a few had steadily gone downhill in production, most had had ups and downs. A few samples of this are shown in Table 45.

TABLE 45.—CASE HISTORIES OF BREEDING FROM BUREAU OF DAIRY INDUSTRY. SURVEY IN TERMS OF YEARLY BUTTERFAT AVERAGES

	Herd A	Herd B	Herd C	Herd D
Foundation cows	318	372	327	435
Daughters of 1st sire	369	366	377	373
Daughters of 2d sire	408	363	421	336
Daughters of 3d sire	495	374	346	291

When it is recalled that the above figures are for the better dairy herds, one can well imagine what the total story on all dairy herds in the United States would be. In general, it would appear that we are breeding our average cows to average bulls, and we can, of course, expect to get average offspring. Better means of discriminating between our own

female lines and sharper tools for use in the selection of males are badly needed.

The most important item in the dairy business is the individual cow. If she is healthy, a good producer, long-lived, and able to transmit her good qualities to her offspring, then there is a firm foundation for the multitude of activities that must result before milk, butter, cheese, or ice cream appear on the consumer's table. If, on the other hand, the individual cow is not healthy, not a good producer, not long-lived, and worse still, probably capable of transmitting these poor qualities to her offspring, then the whole of the dairy industry rests on a very insecure foundation. It is clear, therefore, that dairymen cannot devote too much time and thought to the matter of getting better cows into their dairy herds.

The very first prerequisite for success in dairying or in breeding livestock is that we have healthy animals. A group of dairymen in Middlesex County, Mass., under the leadership of County Agent Herbert Brown organized a herd-health association in 1939. These men pay $1 per cow in advance every 6 months and for this get monthly examinations of the general and genital health of each cow, examinations for pregnancy, treatments for sterility, etc. The herd-health association is designed primarily to prevent rather than to cure diseases, although the latter is sometimes necessary. This is one of the most progressive steps that livestock men have ever taken and deserves emulation in all parts of the United States.

Bases for Judging Production in Dairy Cattle.—The other consideration besides health is that of production, and there are two ways in which probable production is ascertained by the practical dairyman. One is by looking at the animal, studying her type, and arriving at an estimate as to her probable production. The other, and undoubtedly better method, is that of consulting her past records and those of her immediate offspring, ancestors, and collaterals. There is sometimes considerable argument on the question of type *vs.* records. The writer is of the opinion that there should be no argument whatsoever on this score, and there need be none if one will but change the *vs.* to *and.* In other words, dairymen want both good type and good production. There is an accepted standard for type for dairy cattle, and, by and large, this accompanies large production. This is not to say that good type always and necessarily means good production; nor that poor type always means poor production. We are all familiar with the fact that fairly good type cows sometimes fail to be profitable producers. We are also aware of the fact that some cows which fail to meet the ordinary requirements of good type are nevertheless profitable producers. In discussing type, the writer is not thinking so much of fancy, breed points, such as shape and curvature of

horns, perfectly level backs, perfectly set legs, etc.; but he is thinking of general symmetry, dairy quality, and mammary quality and development. There is a decided relation, as numerous statistics show, between size and producing capacity in dairy cattle. Other things being equal, the big cow produces more and returns more over feed cost than does the little cow in any breed or in grade animals. Again, this is not to say that all big cows are good producers and all small cows poor producers. Our experience contradicts such a statement, but it is true that we will more often find high production in big dairy cows that we will in small ones.

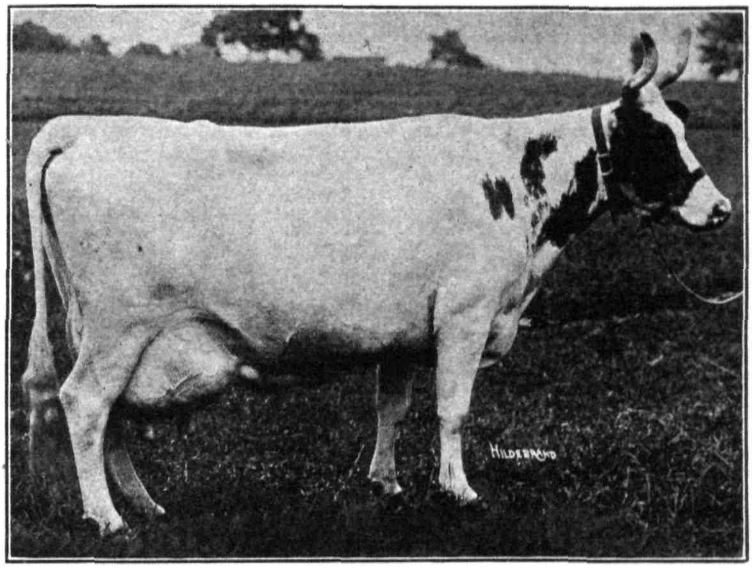

FIG. 163.—Auchenbrain White Beauty 2nd, owned by Penshurst Farm, a splendid example of dairy type.

Therefore, good size for the breed or grade is a point to be kept in mind in the selection of replacements.

The most important consideration as to type is that of dairy quality. By this is meant the form of the external characteristics, which evidence the probable ability and willingness of the animal to consume and digest large amounts of feed beyond her maintenance requirements and the ability also to convert this feed into milk rather than into flesh or fat. These characteristics are evident to the practiced eye, much as they may have been derided by those who like to scoff at type. Among them are a clean-cut face; prominent bright eye; wide strong muzzle; long lean neck; thinness and fineness over the withers; spread between the ribs; length, width and leanness through the rump; leanness through the thighs; fineness of hair and of bone and thinness and mellowness of hide. These

characteristics generally accompany the high milk producer and can be accepted as marks indicative of good dairy production, not, as we have stated above, in an infallible sense, but by and large they will hold true.

Included in size is the matter of length, depth, and width of body. The animals should be deep from the top of the withers to the floor of the chest, should be comparatively wide through the chest region, should be deeper through the rear- than through the foreflank. The ribs should leave the backbone at as much of a right angle as possible and be wide between. Such conformation gives ample room for the vital organs, heart and lungs, and generally indicates the proper bodily mechanism for the consumption and digestion of large quantities of feed.

The third item in addition to size and dairy quality is that of udder quality and capacity. The udder is the working portion of the dairy cow. It should be large. It should be attached well up between the hind legs and well forward on the underline. It should not be broken away and pendulous, and it should have a level sole. The udder should be of good quality; *i.e.*, when milked out, it should be soft and flabby, indicating the presence of enough but no excess connective tissue, which does not, of course, aid milk secretion. The udder of a high-producing cow is generally well-supplied with veins that are evident to the eye. The udder should show as little cleft between the right and left halves as possible, and no cleft between the front and rear quarters as viewed from the side. There should be four teats of uniform size placed toward the four corners of the udder though not, ideally, exactly at the corners.

The blood, carrying food materials to the udder, flows from front to rear along the upper portion of the cow and then descends down through the udder and flows back to the heart, through veins known as the *milk veins*. These veins pass forward from the udder on the underline and should disappear through the body wall somewhere near the front legs. These veins should be large and generally tortuous. If large and tortuous, this can generally be taken as indicating a good flow of blood through the udder. The general type of the dairy cow should indicate strength together with quality. The animals should be of good size but show no coarseness. The practiced eye of the dairyman catches the indication of femininity and quality in a dairy cow. There should be evidence of strength throughout, as indicated by a relatively straight topline, width and depth of chest, straightness and strength of legs when viewed either from the side or the rear. The dairy cow is a hard-working animal, and, if she is to perform her work over a long period of time, she must be of a rugged, strong constitution. At the same time she must show femininity, quality, and animation.

It is relatively easy to separate cows which will produce 4,000 lb. of milk in a year from those which will produce 20,000 lb. of milk in a year.

Nearly everyone handling dairy cows today could do this. It is not so easy, however, to separate cows which will produce 5,000 lb. of milk in a year from those which will produce 8,000 lb. in a year. In fact this is a very difficult job, and a difference of 3,000 lb. in production means the difference between profit and loss in the dairy business—eventually the difference between staying in or being forced out of the dairy business. In order to supplement what we can learn from studying the individuality or type of the animal, we very badly need records when we are purchasing cows.

TABLE 46.—PUBLIC SALE AVERAGE PRICES HOLSTEIN-FRIESIAN CATTLE*
1925–1928, Inclusive

903	cows with long-time records brought	$ 439,430.00	Av. $486.63
1,191	cows with 7-day records brought	311,471.00	Av. 261.54
2,982	cows untested but from tested dams brought	666,499.00	Av. 223.50
5,899	cows untested and from untested dams brought	1,082,909.00	Av. 183.57
575	heifers from long-time record dams brought	156,855.50	Av. 272.80
649	heifers from 7-day record dams brought	102,769.00	Av. 158.33
2,533	heifers from untested dams brought	261,814.00	Av. 103.36
813	bulls from long-time record dams brought	345,736.00	Av. 425.25
730	bulls from 7-day record dams brought	154,258.50	Av. 211.31
1,016	cows from untested dams brought	123,636.50	Av. 121.68
17,291	males and females all ages brought	$3,645,378.50	Av. $210.82

Cows with long-time records brought 165.0% more
Cows with 7-day records brought 42.5% more
Untested cows from tested dams brought 21.7% more than untested cows from untested dams.
Heifers from long-time record dams brought 164.0% more than
Heifers from 7-day record dams brought 53.1% more than heifers from untested dams.
Bulls from long-time record dams brought 249.4% more than
Bulls from 7-day record dams brought 73.6% more than bulls from untested dams.

* Compiled by J. C. Knott, Holstein-Friesian World, Mar. 9, 1928.

If we are purchasing older animals, the best guarantee is production records, either A.R., D.H.I.A., or breed herd-test records. Only in this way can we be absolutely sure of the animal's inherent producing capacity. In the purchase of young animals that have not had lactation periods, one could, of course, get some idea if he knew the average production of the other daughters of the sire of the animal in question, in other words, had production records on her half sisters. He might learn a little something too from her dam's record and more from the records of the paternal half sisters of her dam. Other offspring of the dam can

yield valuable information also. Probably the greatest lack in animal breeding in general today is the lack of records. We will not make as rapid progress in the art of breeding as we might until we get more complete records on our breeding animals. The value of records both on individual animals and their collaterals is well-illustrated many times a year at livestock sales. Records have a dollars and cents value and instead of being a cost and a liability are actually a source of profit and an asset to any livestock breeder. The money spent in securing records is returned to the breeder many times over.

The monetary value of records can be amply demonstrated in any of our purebred dairy-cattle breeds.

Basic Idea in Breeding.—Most dairymen plan to breed their own replacements, and this, in the long run, is by far the safest method for maintaining a healthy herd and for continuously increasing production. To many people, breeding seems like a pretty complicated thing, though, when it is boiled down to its basic principles, it is relatively simple. The second and third sections of this book have presented a detailed discussion of the physiology of reproduction and of the way in which characteristics are transmitted from ancestors to progeny through an animal's immediate parents. We know that any calf arises from the union of one egg and one sperm—the egg produced in the ovaries of the dam, the sperm produced in the testes of the sire. Within these two tiny cells, which even when fused together to start a new life are hardly large enough to be seen with the naked eye, are located the determiners of all the animal's potentialities—whether it will be black and white, red and white, fawn and white; whether it will have horns or be polled; whether it will be of good type or poor type; whether, if well-fed, it will be large or small; whether it will have the capacity for consuming and digesting large amounts of feed and converting this material into milk, or whether the conversion will result in body tissue and fat. All the potentialities of the animals are locked up in two tiny germ cells, which is all any organism gets from its parents. The calf, contrary to a somewhat common belief, gets no blood as such from its mother, but makes its own blood as it grows, just as it makes its own bone, muscle, and other body tissues, blood being a tissue of the body existing in a liquid rather than in a more or less solid state.

Breeding then can be boiled down to the proposition of getting better germ cells. When better eggs are fertilized by better sperm, we will automatically have better animals, and there is no other way to get them. By *better* eggs and sperm is meant, of course, those containing determiners for better characteristics in the resulting offspring. The job of the breeder, then, is to find some way of ascertaining beforehand what the germ cells of a given animal are likely to contain. There are three possible approaches to this problem:

1. Through study of the individual itself and its accomplishments.

2. Through study of the ancestors and collateral relatives of the animal and an attempt to arrive at what those ancestors were most likely to have put into the germ cells.

3. Through study of what actually has come out of the germ cells of a given animal.

In other words, we study the ancestors and the progeny as well as the individual itself. This feature of breeding is the reason for so much stress being laid upon records We keep records mainly to get some factual data on the animals themselves, which in turn may give us some

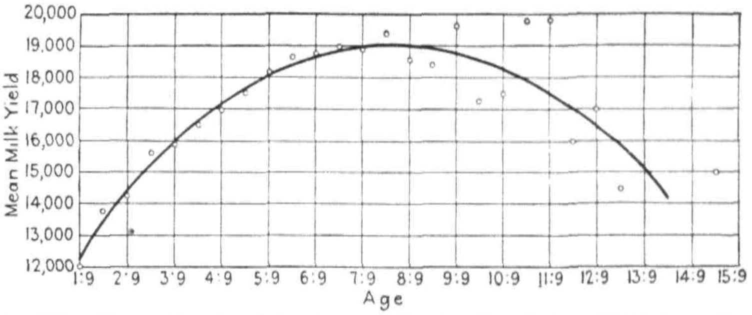

FIG. 164.—Observational and fitted curves showing the relation of 365-day milk yield to age for Holstein-Friesian cattle. The observational curve is represented by small circles. The smooth curve shows the fitted logarithmic curve for milk yield. (*From Gowen, Studies in Milk Secretion, Me. Exp. Sta. Report*, 1920.)

idea of what they are likely to transmit. We will never succeed in breeding better livestock until we keep more accurate records and use them more intelligently after we have secured them.

Conversion Factors.—It is a generally accepted fact that most cows will continue to produce more milk and butterfat yearly from the time they first freshen as two-year-olds up to the age of six to eight years, and that thereafter the amount of butterfat and milk will gradually decline in amount.

TABLE 47.—CONVERSION FACTORS BASED ON ADVANCED REGISTRY REQUIREMENTS

Age Classification, Years	Single-letter Requirement		Conversion Factor		Mature Equivalent
5	400	×	1.00	=	400
4½	381.7	×	1.047	=	400
4	363.4	×	1.100	=	400
3½	345.2	×	1.159	=	400
3	327.0	×	1.223	=	400
2½	308.7	×	1.295	=	400
2	290.5	×	1.376	=	400

The Advanced Registry requirements of our dairy breeds were an early recognition of this fact of increasing production with age. These

requirements state that a cow must make 0.1 lb. of fat in addition for each day that she exceeds two years in age at the time of starting on test. In setting up their increment of increase at 0.1 lb. daily, the purebred dairy-cattle breed associations actually brought age-conversion factors into being.

For some time it has been generally recognized that combined age-conversion factors for all breeds used in compiling dairy herd-improvement association proved-sire data are not entirely satisfactory for converting production records of individual breeds of cows to a mature-equivalent basis.

Until now, however, sufficient data were not available to justify a study of the relationship between age and production by breeds. Through the operation of the Nation-wide Dairy Herd-Improvement Association Proved-Sire Program the States reported 305-day lactation records for permanent recording and data accumulated in sufficient volume so that a study could be made and reliable age-conversion factors for each breed could be developed.

Such a study was made which included the following number of records:

Breed	Number of single records	Number of pairs of records
Ayrshire	16,753	7,385
Brown Swiss	7,793	3,386
Guernsey	65,341	17,392
Holstein	77,464	45,867
Jersey	59,396	18,358
Shorthorn	4,171	1,444

In one part of the study a straight tabulation of single 305-day lactation records of cows of each breed for different ages was compiled. That is, the records of all cows 2 years of age were added and averaged, and so on for the various ages. In another part of the study cows with two or more consecutive lactation records were included in an effort to determine the degree of slope of the production trend line from year to year so as to reduce as much as possible the influence of culling.

Age-conversion factors for each breed were developed by both methods of tabulation. The age-conversion factors developed by the straight tabulation of data for cows at different ages made a larger correction for records of young cows and a smaller correction of records of old cows than did the age-conversion factors computed from the slope of the production trend line derived from paired consecutive records. The two sets of age-conversion factors were tested on records of cows that had a lactation record at approximately 2 years of age and a lactation record made at maturity and on records of cows that had a lactation record at maturity and also a lactation record made at 11 to 12 years of age.

The age-conversion factors based on the paired-consecutive records converted the 2-year-old records and the 11- to 12-year-old records to a mature basis more

comparable to the actual mature records than did the factors developed by a straight tabulation of records of cows of different ages. Age-conversion factors based on paired-consecutive records were, therefore, assumed to be more reliable.

The age-conversion factors for the Ayrshire, Jersey, and Guernsey cows were not significantly different. For practical use and simplicity the three factors were combined. The factors for Brown Swiss and Milking Shorthorn cows were similar. Inasmuch as the Shorthorn factors were based on relatively meager data, Brown Swiss data were used to develop combined age-conversion factors for Brown Swiss and Milking Shorthorn cows. The Holstein factors were significantly different from the factors for any other breed. Factors for Ayrshire, Guernsey, Jersey and Holstein cows were combined to develop a set of factors for converting records of cows of mixed breeding.

TABLE 48.—AGE-CONVERSION FACTORS, D.H.I.A. DATA

Age	Ayrshire, Guernsey, Jersey	Brown Swiss. Milking Shorthorn	Holstein	Mixed average of Ayrshire, Guernsey, Jersey, and Holstein
1–6	1.343	1.718	1.515	1.429
2–0	1.262	1.538	1.377	1.319
2–6	1.195	1.400	1.275	1.235
3–0	1.141	1.286	1.203	1.172
3–6	1.099	1.196	1.131	1.115
4–0	1.063	1.136	1.077	1.070
4–6	1.037	1.088	1.035	1.036
5–0	1.020	1.052	1.017	1.018
5–6	1.008	1.028	1.006	1.007
6–0	1.000	1.012	1.000	1.000
6–6	1.000	1.006	1.000	1.000
7–0	1.000	1.000	1.006	1.003
7–6	1.006	1.000	1.012	1.009
8–0	1.012	1.000	1.018	1.015
8–6	1.018	1.000	1.036	1.027
9–0	1.024	1.006	1.054	1.039
9–6	1.035	1.012	1.072	1.053
10–0	1.047	1.030	1.090	1.068
10–6	1.064	1.048	1.114	1.089
11–0	1.082	1.072	1.138	1.110
11–6	1.100	1.096	1.162	1.131
12–0	1.112	1.114	1.192	1.152
12–6	1.124	1.132	1.222	1.173
13–0	1.136	1.144	1.252	1.194
13–6	1.148	1.156	1.282	1.215
14–0	1.160	1.168	1.306	1.233
14–6	1.172	1.174	1.330	1.251
15–0	1.184	1.180	1.348	1.266
15–6	1.193	1.186	1.366	1.279
16–0	1.199	1.192	1.378	1.288

The above age-conversion factors based on paired consecutive records are recommended for use in Dairy-Herd-Improvement Association Proved-Sire Work.

The Bureau of Dairy Industry considers that milking a cow 4 times a day increases her production 35 per cent and milking her 3 times a day increases her production 20 per cent over what it would have been on twice-a-day milking.[1]

To convert a 365 day record to a 305 day basis multiply by	0.85
To convert a 305 day record to a 365 day basis multiply by	1.17
To convert a 4 times a day milking to 3 times a day milking multiply by	0.88
To convert a 4 times a day milking to 2 times a day milking multiply by	0.74
To convert a 3 times a day milking to 4 times a day milking multiply by	1.13
To convert a 3 times a day milking to 2 times a day milking multiply by	0.83
To convert a 2 times a day milking to 3 times a day milking multiply by	1.20
To convert a 2 times a day milking to 4 times a day milking multiply by	1.35

To convert 2 milkings per day for 305 days to 3 milkings per day for 365 days add 40 per cent.

To convert 3 milkings per day for 365 days to 2 milkings per day for 305 days subtract 30 per cent.

Since cows are sometimes milked three or four times a day for a portion of a lactation and these extra milkings lead to increased production, it becomes necessary to have conversion factors which will standardize such records to a twice-a-day milking basis. These factors, shown in Table 48*A*, are applied after the cow's record has been standardized to a mature-equivalent basis by the use of the factors found in Table 48.

If a cow is milked four times a day for 35 days and three times a day for 50 days, the record is first converted to a mature-equivalent basis by using the appropriate age factor in Table 48. The number of days she was milked three times daily is then multiplied by 0.6, in order to convert these three times daily milkings to a four times daily basis, and this figure is added to the number of days the cow was milked four times a day. In the above case we would have $50 \times 0.6 = 30 + 35 = 65$ days of four times a day milking, which means that the original age corrected record would have to be multiplied by 0.9306 (Table 48*A*) in order to compensate for 50 days of three times a day milking and 35 days of four times a day milking and thus bring the record down to its equivalent of twice-a-day milking for the 305-day milking period.

In a study of 2,900 purebred cows (all breeds) with D.H.I.A. records and 40,000 purebred cows with official records, Gifford found that D.H.I.A. records would have to be multiplied by 1.43 for two-year-olds up to 1.83 for thirteen-year-olds, with an average for all ages of 1.68, in order to bring them up to a comparable basis with records made under

[1] Paper presented by J. F. Kendrick, Division of Dairy Herd Improvement Investigations, Bureau of Dairy Industry, before the Extension Section of the *Amer. Dairy Sci. Assoc.*, Burlington, Vt., June 23 to 26, 1941.

official test. Likewise, to scale down official records to a comparable D.H.I.A. basis, the factors were 0.70 for two-year-olds and 0.55 for thirteen-year-olds, with an average figure for all ages of 0.59. Eckles, Anthony, and Palmer state that "official test conditions gave an increase of 70 per cent in milk over good farm conditions."

TABLE 48*A*.—FACTORS FOR REDUCING PRODUCTION RECORDS TO A TWICE-A-DAY MILKING BASIS

Number of days milked	3 times daily	4 times daily
5–15	0.9903	0.9831
6–25	0.9839	0.9721
26–35	0.9776	0.9614
36–45	0.9713	0.9509
46–55	0.9652	0.9406
56–65	0.9591	0.9306
66–75	0.9531	0.9208
76–85	0.9472	0.9111
86–95	0.9414	0.9017
96–105	0.9356	0.8925
106–115	0.9299	0.8834
116–125	0.9242	0.8746
126–135	0.9187	0.8659
136–145	0.9132	0.8573
146–155	0.9077	0.8490
156–165	0.9024	0.8408
166–175	0.8971	0.8328
176–185	0.8918	0.8249
186–195	0.8866	0.8171
196–205	0.8815	0.8096
206–215	0.8764	0.8021
216–225	0.8714	0.7948
226–235	0.8665	0.7876
236–245	0.8616	0.7806
246–255	0.8567	0.7736
256–265	0.8520	0.7668
266–275	0.8472	0.7601
276–285	0.8425	0.7536
286–295	0.8379	0.7471
296–305	0.8333	0.7407

Gaines has raised the question as to whether corrected milk yields are better indicators of the genetic complex of our cows than are the actual

records. His study, based on 29 sires with 8 to 36 daughters listed in Volume VI of the Herd Improvement Register Yearbook of the Holstein-Friesian Association of America, showed that the correlations between the first and second lactation records of a cow, between first and third, second and third, second and first, and third and second were smaller for the corrected records than for the actual records and with individual correlations ranging from +0.98 to −0.68.

Gaines suggests the following plan to obviate the necessity for using correction factors:

A plan is recommended, in its own right and to dispose of the correction problem. It is based on the present herd test system of continuous testing, with the addition of live weight of the cow at the start of each lactation. The plan is to deal with each lactation on the basis of calories of milk energy, per kilogram initial live weight of the cow, per day for the first eight monthly tests of the lactation. For reference this expression may be abbreviated to Cals./Kgs./Ds., or C-K-D. Milk energy is estimated from the records of milk and fat percentage, for example, calories = kgs. milk × (2⅔ + fat %) × 112.5 = kgs. milk × 300 + gms. fat × 11.25, etc., the correlation between actual and estimated calories being of the order r = .99, so far as accuracy of the equation is concerned.

C-K-D is frankly a technical measure of lactation, intended for purposes of biological analysis. It may be translated directly into very practical terms as pounds of 4% milk, per 1000 pounds live weight, per day over the normal calving interval. This assumes the normal-calving-interval daily milk energy yield to be 75 per cent of the daily milk energy yield for the first 8 months of the lactation. Thus, C-K-D = 30 is the same as 40 pounds 4% milk, per 1000 pounds live weight, per day for 8 months; and corresponds approximately to 30 pounds 4% milk, per 1000 pounds live weight, per day for the normal calving interval.

On evidence as yet only in part conclusive, it is postulated that for practical purposes in improved dairy cattle, C-K-D may be considered as independent of:

1. Service period and length of lactation
2. Age of cow at start of lactation
3. Fatness of cow at start of lactation
4. Live weight of cow at start of lactation
5. Composition of milk for the lactation
6. Breed of cow

Considering the cow as a machine for the conversion of feed energy into milk energy the plan contemplates the use of 3 values, considered as mutually independent:

1. Live weight of cow, or size of machine
2. C-K-D, or working efficiency of machine
3. Fat percentage, or kind of work of machine

In addition there should be some quantitative appraisal of surroundings—feed, care, etc. Number of milkings is an item in such an appraisal, but in itself hardly comprehensive enough. The use of corrections for number of milkings is

particularly questionable when applied to the daughters of an individual sire. And it is the performance of this small group of daughters with which we are most vitally concerned in breeding.

The benefit of correction factors applied to milk yields, as giving a better estimate of germ plasm or genetic make-up of the cow, is very dubious, judged by certain herd test records of the Holstein-Friesian Association. The correlation between various records of the same cow is lower for the official corrected records than for the official actual records. As between individual sire daughter groups (the field within which the dairyman must work) the actual correlations range from $r = +.982 \pm .007$ to $r = -.60 \pm .15$, with an average value of about +.3. A plain lesson is the necessity of continuous or lifetime records under a plan that avoids correction factors.

A plan is recommended, in its own right and to dispose of the correction problem. It is based on the herd test system with the addition of live weight of the cow, and considers the first 8 months of each lactation on the basis of milk energy per unit initial live weight. The plan regards the cow as a machine to convert feed energy into milk energy and considers 3 mutually independent values: 1. Live weight, or size of machine. 2. Calories per kilogram per day, or working efficiency of machine. 3. Fat percentage, or kind of work of machine.[1]

What we are actually interested in in our dairy cattle is the amount of feed energy that they can transform into milk and butterfat and the efficiency with which they do it. From Gaines's study as well as from a logical standpoint, it is obvious that we should use continuous or lifetime records rather than single lactation records in estimating the genetic make-up of our cows and in indexing bulls. The best measure would perhaps be the amount of 4 per cent fat-corrected milk (amount of milk × 0.4 + amount of fat × 15) produced per day for a cow's lifetime, for this would also bring into the picture such things as reproductive efficiency, length of service period, etc., as well as maximum yield during the lactation period, persistency, etc.

The technique of analysis of variance, by means of which it is possible to sort out the genetic from the environmental and other causes of the variation found in measurable characters that are easily subject to environmental influences and to estimate how much of the variation is due to each cause, is revealing the fact that about half of the variation of this sort (yield of milk or wool, rate of gain, etc.) is due to environmental causes and half to the individuality of the animal. Much of the latter is also environmental in the sense that feeding and management along with other environmental factors greatly influence the ultimate size of the animal. Perhaps only 10 to 30 per cent of the commercially valuable characters of our animals are determined, in the final analysis,

[1] GAINES, W. L., Correction Factors and Germ Plasm in Dairy Cattle Breeding, *Amer. Soc. Anim. Prod. Proc.*, pp.50–53, 1935.

by the genetic contributions of their parents. If this is so, then it would hardly seem necessary after all to compare daughters' and dams' production to get a bull's index, but rather the average production of a bull's daughters could serve equally well or better as his index. Thus, if we secured the indexes of bulls A and B on the production of their first 6 to 10 daughters when they milked as two-year-olds, we would not need conversion factors. This, of course, leaves out of account seasonal variations, which may be very large at times, as well as the greater accuracy secured from the use of lifetime averages. It is quite evident that we have not yet reached the end point in the evolution of bull indexes and conversion factors.

For the present, we will probably continue to apply correction factors but with the hope that they can be still further refined and that the necessity for their use can perhaps eventually be done away with.

Systems for Indexing Bulls.—Realization of the inadequacy of type and pedigree as selection indexes for dairy cattle has recently focused attention on the proved-sire idea. Now a proved bull is one with a certain (varying according to different investigators) number of daughters with records out of dams with or without records (again according to the ideas of various investigators). In general, the idea is to get a genetic picture of the bull by studying his mates and daughters, for the bull himself gives no milk.

Although it is generally accepted that the amount of milk which a cow yields is not necessarily an accurate representation of her genetic make-up in this respect, nevertheless, the record is tangible evidence of a sort and can be dealt with directly. In the case of the bull, however, there is no such tangible evidence, for he yields no milk, and his transmitting ability must necessarily be dealt with indirectly. This fact has led to various attempts during the past few years to formulate a bull index that would represent the bull's transmitting ability for amount of milk and percentage of fat. The following seven hypotheses have been suggested for indexing bulls.

1. Pearl, Gowen, and Miner[1] (1919) suggested the quartile method of arriving at a bull's transmitting ability. This method consists of plotting the curve of variability of Advanced Registry records, dividing it into quartiles (or octiles), then classifying the offspring of each sire in terms of percentage on the basis of the relative standing of each dam with her daughter. The highest quarter of the Advanced Registry records was called *A*, the second *B*, the third *C*, and the fourth *D*. If a bull had 4 daughters, and 50 per cent, or 2, of them were in the second quarter, whereas the respective dams were in the first quarter; 1 daughter, or

[1] Pearl, R., Gowen, J. W., and Miner, J. R., *Maine Agr. Col. Ext. Bul.* 281 (Studies in Milk Secretion VII), 1919.

25 per cent, was in the second quarter, whereas her dam was in the third quarter; and 1 daughter, or 25 per cent, was in the fourth quarter, whereas her dam was in the first quarter; the bull was then represented by the following formula, the dams' letter being given first;

$$50AB + 25CB + 25AD.$$

The example just given seems relatively simple, but on occasion this formula for a bull can become very complicated, *e.g.*, the formula for Spermfield Owl,

$$12AA + 4AB + 4AC + 23BA + 12BB + 4BC + 8CA + 8CB + 4CD + 12DA + 4DB + 8DD.$$

In any event, the method is very complicated and too indefinite for general use. In any given case the question for which a breeder seeks an answer is, How many pounds of milk and what fat percentage will this bull transmit to his daughters? No such definite answer is possible by the quartile method.

2. Yapp[1] (1925) advanced the theory that a sire's potential transmitting ability might be expressed in terms of 4 per cent milk by the formula $X = 2A - B$. Here X = the sire's potential transmitting ability, A = the daughters' average records converted to a 4 per cent fat basis, and B = the dam's record converted to a 4 per cent fat basis. This is tantamount to saying the average production of the daughters falls just halfway between the average production of the dam's and sire's potential transmitting ability. We have here the adoption of the theory, borne out quite generally in nature, that the crossing of two extremes will produce progeny about halfway between the parents if and when the character is determined by multiple factors, as no doubt milk production is. Genetically, this is based on the theory of blending inheritance. It is comparatively simple, of course, to find the bull's index provided the dams' and the daughters' average productions are known. This method is unfortunate in that it hides in one figure details that a breeder should know, *viz.*, the potential amount of milk and the percentage of fat which the bull transmits. The method of converting records to a 4 per cent basis as practiced by Yapp was based on the following formula derived by Gaines and Davidson[2] from a study of the energy conversions of dairy cattle, said formula being 0.4 of the milk plus 15 times the fat equals the fat-corrected milk to a standard 4 per cent basis.

[1] YAPP, W. W., Transmitting Ability of Dairy Sires, *Amer. Soc. Anim. Prod.*, reprint *Ann. Proc.*, December, 1924.

[2] GAINES, W. L., and DAVIDSON, F. A., Relation between Percentage Fat Content and Yield of Milk, *Ill. Agr. Expt. Sta. Bul.* 245, 1923.

The following table[1] gives the factors for standardizing milk of any test to a 4 per cent fat-corrected milk basis.

TABLE 49.—FACTORS FOR CONVERTING WEIGHTS OF MILK OF OTHER FAT CONTENT TO THEIR ENERGY-EQUIVALENT WEIGHT OF 4.0 PER CENT MILK

*f**	0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
2	0.700	0.715	0.730	0.745	0.760	0.775	0.790	0.805	0.820	0.835
3	0.850	0.865	0.880	0.895	0.910	0.925	0.940	0.955	0.970	0.985
4	1.000	1.015	1.030	1.045	0.060	1.075	1.090	1.105	1.120	1.135
5	1.150	1.165	1.180	1.195	1.210	1.225	1.240	1.255	1.270	1.285
6	1.300	1.315	1.330	1.345	1.360	1.375	1.390	1.405	1.420	1.435
7	1.450	1.465	1.480	1.495	1.510	1.525	1.540	1.555	1.570	1.585

* *f* = fat percentage.

3. Turner[2] (1925) proposed the following formula as a means of ascertaining a bull's index: Sire's potential transmitting ability equals the daughter's fat production minus 0.15 of the dam's fat production divided by 0.85. This formula grew out of Turner's study in which he found that for each increase of 100 lb. of fat on the part of the dams the daughters increased 15 lb. This formula of Turner's implies the genetic theory of partial dominance on the part of the bull, since the daughters are seen to progress 85 per cent of the way up or down to the bull's level from the dam's average level of production.

4. Graves[3] (1926) suggested comparing the dams' and daughters' records and letting the difference (plus or minus) stand for the bull's index. In rating bulls under this system Graves also considered the average milk production of the dams and daughters, the average fat percentage of the daughters and the dams, and the percentage of daughters making an increase in amount of milk as well as the percentage making an increase in fat test.

5. Goodale[4] (1927) from a study of Dr. Gowen's[5] crossbreeding experiments with cattle, proposed the Mt. Hope bull index.

Dr. Gowen found, as have others, that the milk yield of the first generation daughters of a cross between a high producing breed and a low producing breed,

[1] PERKINS, A. E., A Simplified Procedure for Calculating Weights of Milk, etc., *Jour. Dairy Sci.*, **20**: 129–132, 1937.

[2] TURNER, C. W., A Comparison of Guernsey Sires, *Mo. Agr. Expt. Sta. Res. Bul.* 79, 1925.

[3] GRAVES, R. R., Transmitting Ability of 23 Holstein Friesian Sires, *U.S. Dept. Agr. Bul.* 1372, 1926.

[4] GOODALE, H. D., Selecting a Herd Sire, Mt. Hope Farm Publication, 1927.

[5] GOWEN, J. W., Inheritance in Crosses of Dairy and Beef Breeds of Cattle, *Jour. Hered.*, Vol. 11, No. 7, 1920. (Milk) *Ibid.*, No. 8.

is intermediate between the parental levels but not exactly half-way, being nearer the high level than the low level. [The inherent fallacy here is that the bull's level is an arbitrary figure, *i.e.*, must be since the bull produces no milk.] Fat per cent, in the case of a cross between breeds of high and low fat production, is also intermediate between the parental levels, but unlike milk quality tends to approach the low level. These experiments have led to the conclusion that in matings between animals of unequal levels milk production is on the average about seven-tenths of the distance above the level of the lower parent, while butter-fat per cent is about four-tenths of the distance above the lower level.

Believing that what is true for crosses between breeds might also be true for matings within a breed, Dr. Goodale made a study of the transmitting ability of the 68 Jersey sires having five or more daughter-dam pairs, which are listed in bulletin 281 of the Maine Agricultural Experiment Station, also of the 58 sires of various breeds listed in Circular 368 of the United States Department of Agriculture and of a large series of Guernsey bulls worked up by the staff at Mount Hope Farm. On the basis of these records the bull index was formulated as follows:

MOUNT HOPE INDEX—MILK

Compute the average mature equivalent of the milk production of all daughters of the bull; also the average mature equivalent of the milk production of the dams of these daughters and take the difference between these averages.

If the daughters' average exceed the dams' average, add three-sevenths (or .4286) of the difference to the daughters' average to get the bull's milk index figure.

If the daughters' average is less than the dams' average, subtract seven-thirds (or 2.333) of the difference from the daughters' average to get the bull's milk index figure.

MOUNT HOPE INDEX—BUTTERFAT, PER CENT

The index for percentage of butterfat is obtained by similar operations, but with different fractions.

If the daughters' butterfat average percentage exceeds the dams' butterfat average percentage, add three-halves (or 1.5) of the difference to the daughters' average to get the bull's butterfat index.

If the daughters' average is less than the dams' average, subtract two-thirds (or .6667) of the difference from the daughters' average to get the bull's index.

6. Gifford[1] (1930) from a study of a group of Guernsey bulls concluded that the daughters' records could be used as the index of the bull. In other words, the dam's contribution is disregarded entirely, which is all right provided the dams in each instance are an average of the breed.

[1] GIFFORD, W., The Mode of Inheritance of Yearly Butterfat Production, *Mo. Agr. Expt. Sta. Res. Bul.* 144, 1930.

7. Wright[1] has proposed a method for evaluating bulls that takes into account the number of daughter-dam pairs available. He has clarified the situation by distinguishing between three types of matings. The first type, a mating of a bull with some individual cow, Wright says, can be answered by using the method of multiple regression, provided all of the necessary correlation coefficients are available. Even this, however, would seem to be rather a risky procedure in the present state of probable heterozygosity of most of our dairy animals. The second type of matings of a bull to cows in the same herd or of similar levels of production, Wright says, can be foretold by the records of the previous daughters of the bull.

For the answer to the question as to what record would be expected of daughters of a bull, if the latter were mated with a random sample of cows of the breed, Wright has proposed the following formula:

$$S = \frac{2}{n+2} A + \frac{n}{n+2} (2O - D)$$

where n = the number of daughter-dam comparisons; A = the breed average in production; O = the daughters' average production; D = the dams' average production; and S = the bull's index. This system is based on the genetic theory of multiple-factor inheritance and gives added weight to the breed average, where the number of daughter-dam comparisons is small and increasing weight to the daughter-dam comparisons as the number of these increases.

At the present time, the dairy-bull index that is being most used is the one which places the daughters exactly halfway between the production level of their dams and the index of their sire, both for amount of milk and percentage of fat. This is known under various names, *e.g.*, American, equal-parent, intermediate, and modified Mt. Hope. First we must convert the milk records of cows to which a bull was mated to some standard basis by means of conversion factors given above; do the same thing to the daughters' records; and, when we have gotten all the records onto a comparable basis, make a comparison between the average production of the dams and the average production of the daughters. For example, if a bull was bred to cows that averaged 7,000 lb. of milk and the daughters averaged 8,500 lb. of milk, then the bull's index would be 10,000 lb. of milk, letting the daughters fall just halfway between the actual average production of the dams and the estimated index of the bull, on the assumption that both parents are jointly and equally responsible for the characteristics of their offspring. Likewise, if a bull was bred to cows that averaged 7,000 lb. of milk

[1] Wright, S., On the Evaluation of Dairy Sires, *Amer. Soc. of Anim. Prod. Proc.*, 1931, pp. 71–78.

and the daughters averaged 6,000 lb. of milk, then the bull's index would be 5,000 lb.

The index for fat test is figured in exactly the same way. In other words, if the dams averaged to test 4.3 and the daughters averaged to test 4.5, then the bull's index for test would be 4.7. The index on a bull is a very useful tool in the selection and breeding of dairy animals, though by no means the only one. Figure 165 shows the index of a given bull with the dams' records on the left and the daughters' records on the right, both sets converted to standard mature age, six years, 305 days

Dams					Daughters				
Age of cow	Actual record	Conversion factor	Converted record	Test	Age of cow	Actual record	Conversion factor	Converted record	Test
2	7,841	× 1.262	= 9,895	4.91	3½	7,422	× 1.099	= 8,157	5.21
2	8,263	× 1.262	= 10,428	5.06	4	8,347	× 1.063	= 8,873	5.10
3½	9,340	× 1.099	= 10,265	4.83	2	7,250	× 1.262	= 9,149	5.00
6	11,521	× 1.000	= 11,521	5.21	3½	9,351	× 1.099	= 10,277	4.98
4	10,842	× 1.063	= 11,525	4.96	2½	10,461	× 1.195	= 12,500	5.03
6	9,560	× 1.000	= 9,560	5.01	3	7,340	× 1.141	= 8,375	5.12
			6/63,194	6/29.98				6/57,331	6/30.44
			10,532	4.99				9,555	5.09

All records—305-day lactations

Average of dams	10,532 − 4.99
Average of daughters	9,555 − 5.09
Difference	− 977 + 0.10
Bull's index	8,578 − 5.19

FIG. 165.—Bull-index work sheet. For a worth-while index the first 6 to 10 daughters of a bull must be tested and their average production compared with that of their dams. We could select 6 daughters of almost any bull and thereby give him a fairly high index, which might have a large advertising value, but its genetic value would be almost zero. Average production over a period of years gives a much truer estimate than does the production of any one year.

lactation, twice-a-day milking. Since records show that the fat test of milk produced by a cow is relatively constant, *i.e.*, changes little if at all with age, it is not customary or necessary to apply any conversion factors to the butterfat test. The bull comes out with an index of 8,578 lb. of milk and a 5.19 per cent on 6 daughter-dam pairs. It would have been better, of course, for the bull to have had 10 daughters rather than 6, and they must be the first 6 or 10 daughters; *i.e.*, they cannot be a selected 6 or 10 and give us anywhere near accurate results.

Breeder Must Know His Own Herd First.—When a breeder starts out to look for a dairy bull, he must look first through his own herd

and know the actual average production of the cows in his herd. The reason for this lies in the fact that a breeder might find a bull with an index of 10,000 lb. of 4.6 per cent milk, and the question arises as to whether or not this is a good bull for this breeder to use. If the breeder's herd average is 7,000 lb. of 4.0 per cent milk, then this would be an excellent bull to use from a production standpoint, because he should tend generally to pull the daughters up halfway between 7,000 and 10,000, or up to the 8,500 lb. level on the average, and he should pull the fat test up to 4.3 per cent on the average. On the other hand, if the breeder's herd average was 13,000 lb. of 5.0 per cent milk, then this bull would be a decided detriment in his herd. In other words, the value of a bull depends on the level of production of the herd in which he is to be used. In one herd the bull may be worth many hundreds of dollars; in another herd the same bull may be a liability right from the start, depending on the level of production of the cows in the two herds.

Besides knowing the average production of his own cows, a breeder should study their conformation very carefully. It will often be found that some common fault runs through most of the cows, such as crooked hind legs, pendulous udders, weak backs, etc. In selecting a sire, it is a wise precaution to try to select one that is particularly strong where the females are weak and one that comes from a family which is strong in this regard.

Dairy-cattle Pedigrees.—In selecting a bull, care should be exercised to see that we get one with a good pedigree, and this refers not so much to names in the pedigree but rather to records. Selecting a bull on the basis of his dam's record will not get us very far. The records of the dams of a large group of low-indexed bulls in one of the breeds recently studied by the writer were just as large on the average as the records of the dams of bulls with very high indexes. Dams' records are all right as far as they go, but they don't go very far.

What is meant by good and poor pedigrees is illustrated in Figs. 166 and 167. Figure 166 shows a bull with a lot of material in his pedigree, but there is no opportunity to ascertain from this material the probable transmitting level of the bull. The other pedigree is a good one because it is possible to ascertain from this material what the probable transmitting ability of the young bull is.

The fraction preceding the bulls' indexes in the pedigree (Fig. 167) indicates by the numerator the number of daughter-dam pairs that were used in securing the index; by the denominator the total number of daughters of the bull in question. The fraction following the bulls' indexes indicates by the numerator the percentage of the daughters exceeding their dams in milk production and by the denominator the percentage of daughters exceeding their dams in fat test. The pedigree

- Sire of Calf:
  A
  - C
    4 daughters average, mature basis
    16,341—611—3.74
  - D
    2 yr. 2 mo. Cl. A.
    18,105—658
    3 yr. 4 mo. Cl. A.
    23,229—828
    - G
      22 A.R. daughters
- Dam of Calf:
  B
  3 yr. 6 mo. Cl. B., 305 days
  13,294—453—3.4
  - E
    25 daughters average, mature basis
    22,121—768
  - F
    2 yr. 7 mo. Cl. B., 305 days
    9,611—323—3.3
    4 yr. 5 mo. Cl. A., 365 days
    22,123—718—3.2
    - H
      4 A.R. daughters average, mature basis
      24,417—845

FIG. 166.—A pedigree that gives no insight into what may be present in the germ cells of this bull calf (see also Fig. 159).

- Sire of Calf:
  A
  Index
  $\frac{32}{36}$ 15,000—5.2 $\frac{67}{75}$
  Range Dams 6,000–17,000
  Daughters 10,000–14,000
  - C
    Index
    $\frac{20}{24}$ 12,480—4.9 $\frac{50}{63}$
    Range Dams 7,000–10,000
    Daughters 8,000–15,000
  - D
    Average two lactations 10,680—5.2
    1 daughter averaged two lactations 14,640—5.0
    - G
      Index
      $\frac{61}{72}$ 13,560—4.9 $\frac{58}{69}$
      Range Dams 7,000–18,000
      Daughters 8,000–11,000
- Dam of Calf:
  B
  Average five lactations 12,500—5.1
  3 daughters average six lactations 13,300—5.2
  2 proved sons—which substantially increased daughters over dams
  - E
    Index
    $\frac{15}{20}$ 14,175—5.4 $\frac{41}{82}$
    Range Dams 8,000–14,000
    Daughters 9,000–13,000
  - F
    Record 15,170—5.1
    4 daughters average ten lactations 14,610—5.0
    - H
      Index
      $\frac{41}{50}$ 12,680—4.8 $\frac{47}{40}$
      Range Dams 9,000–12,000
      Daughters 8,000–15,000

FIG. 167.—A pedigree that gives a fairly good insight into what may be present in the germ cells of this fictitious bull calf.

in Fig. 167 gives a lot of information about the probable transmitting ability of this young bull. The other pedigree gives us nothing, and we might just as well draw a bull out of a hat with our eyes closed.

Nothing as yet has been said about the type in the bull, but it is obvious that we want indications of good type in the bull just as much as we do in the females, and the indications are the same as those mentioned earlier for the cow, particularly the matter of dairy quality as indicated by a long relatively lean neck, pointed withers, width between

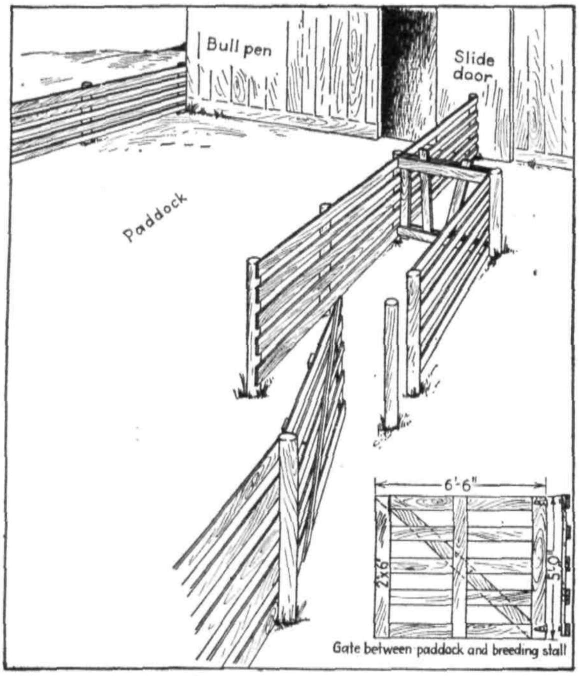

FIG. 168.—Any bull is "safe" in this sort of pen. (*From Univ. Wis. Ag. Exp. Sta. Circ.* 238.)

the ribs, length and levelness of rump, thinness through the thighs, deep, wide body, and quality as indicated by thin skin and fine hair and bone. Along with these dairy qualities should go, of course, evidence of strength, masculinity, and alertness, and the bull should be strong in bodily character where the cows in the breeder's herd tend to be weak.

Age of Bull to Buy.—It seems fairly obvious that the best buy in a bull would be a proved sire, one that had already demonstrated his ability to transmit good type, production, and all the other desirable things which we want in a herd of dairy cattle. If the bull has done a good job of transmitting in one herd, he stands a pretty good chance of

doing likewise in another herd, but this is not an absolute certainty. Some bulls do well in one herd, not very well in some other herd, and the reverse of this occasionally happens too. If management is adequate in both herds concerned, the differing transmitting abilities of bulls is probably genetic. As the breeders say, the bull "nicked" well here, he didn't there. In other words, the genes of the bull fitted well with the genes of the cows of one herd but not with those of the other.

There are several difficulties with good adequately proved bulls: (1) There are not many of them, (2) their price is apt to be high, (3) they are often getting on in years and losing some of their breeding vigor and sureness, (4) they are often dead when we learn of them.

In other words, although good proved bulls are the best bet, few of us are going to be apt to use them. Most of us, in other words, are going to be using young bulls for some time to come.

If we can't get a proved sire six or eight years old, should we buy a younger bull, say three or four years old? Some breeder may have such a bull and not want to use him on his own daughters but be anxious to keep him alive. If the bull has a good pedigree, if his daughters look good in comparison with their dams, if the herd is clean, so that we are not apt to be introducing disease into our herd by the use of this bull, and if he can be purchased at a reasonable price or, better still, leased at a nominal price, or if perhaps you find yourself in a similar situation to this breeder, you two might then just exchange bulls for 1 or 2 years, and the bull problem would be solved for a while.

And so we might go on, all the way down to calves. A six- or eight-year-old bull might be proved, a four-year-old might have a group of daughters just starting to freshen, a three-year-old bull might have a group of yearling daughters, a two-year-old bull a bunch of calves being born, a yearling bull will have no offspring, but he has had a chance to grow out a bit so we can get an idea about what he is going to look like. With the calf, there is not much that we can determine perhaps except that he is alive and with good luck ought to remain so for some time.

There are dangers and possible disappointments in the purchase of any male. The problem is worthy of all the study and effort we can put into it.

The principal dangers with the purchase of older bulls are both physiological and genetic. In other words, the older bull used in some other herd may bring disease with him when he comes to us, and it is very easy to draw rather broad conclusions from rather few data. Perhaps a bull has half a dozen daughters that in their youth look a lot better than their dams which have seen a lot of hard service, but how will 30 of his daughters look 5 or 8 years from now. It is very easy to fool ourselves with a small number of young offspring.

With a bull calf, we generally largely avoid the matter of his introducing disease into our herd. Genetically, we can know nothing about him except what we can guess from his pedigree and his collateral relatives. The older bull gives us a chance to see a few of his offspring—generally too few and too young to be a very sure indication. The young bull, although having no offspring, is generally on the farm where he was bred. We, therefore, usually have a chance to study his sire and dam, often many other of their offspring and other direct or collateral relatives of the bull calf in question. Also the calf can usually be bought more cheaply.

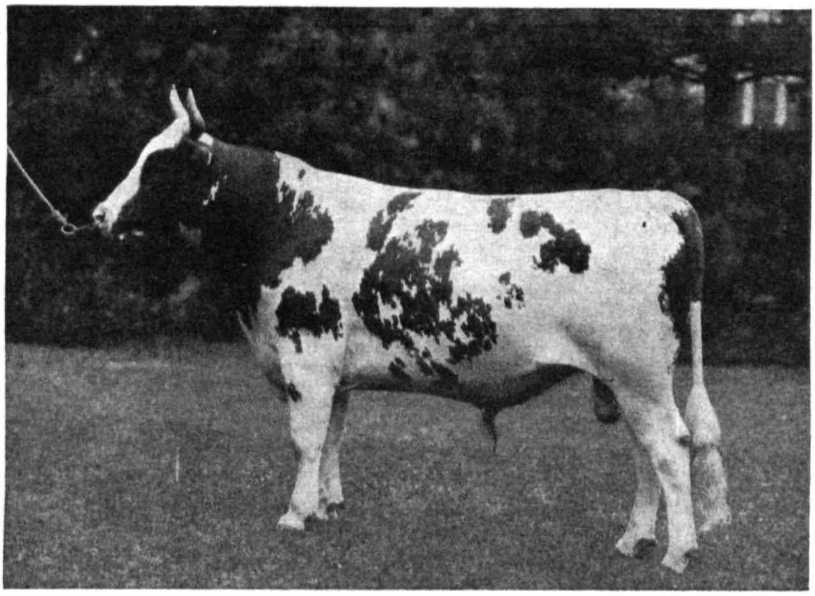

FIG. 169.—The great Ayrshire bull, Man O'War, whose 150 daughters, at an average age of 3.4 years, average on a mature equivalent basis 14,540 lb. of 4.10 per cent milk (*Courtesy of Penshurst Farm, Narberth, Pa.*)

There is no definite categorical answer to the question—is it better to buy a two- to four-year-old bull or a bull calf—provided a good definitely proved bull is not available. There are many angles from which the problem can be profitably viewed, and the solution will vary with different individuals and circumstances.

One thing is certain, we need to prove more bulls. Records show that, on the average, out of every three bulls, one will give daughters that excel their dams in production, one bull's daughters will produce less than their dams, and one bull's daughters will produce at the same level. When a young bull is purchased, he preferably should be used on 12 or 15 cows when he is just at or past a year old and then be leased,

loaned, or just temporarily retired until 5 or 6 of his daughters have made records. In this way the good transmitting bulls can be discovered and, when discovered, used as extensively and as long as possible. The present system is generally the exact opposite of the above. A bull calf is purchased, he gets one to two crops of calves, and then he goes to the butcher to avoid inbreeding. Thus lots of good young bulls have been real "boloney" before their worth was realized, and by the same token lots of poor bulls get by on the "phony" "boloney" of 6 or 8 good daughters out of a total crop of 60 or 80 daughters.

Saying that we need to prove more bulls (and keep them alive till proved) is another way of saying that we need more records. Records of production of daughters compared with records of production of their dams will give us a bull index. The index figure itself, however, is not enough. We need both the daughters' and the dams' production to see what made the index. An index of 11,000 lb. of milk might be due to a bull having been bred to 7,000-lb. cows and getting 9,000-lb. daughters. It might also be due to a bull having been mated to 17,000-lb. cows and getting 14,000-lb. daughters. Both indexes are the same, *viz.*, 11,000 lb. Presumably, if the index idea is sound, these bulls are somewhat alike genetically. Some would say they are just alike (from a production standpoint), but others want to take this with a rather liberal-sized grain of salt. We would prefer the former bull, the one that had raised production, to the other. At least we must have both dams' and daughters' production, and we must know whether these daughters were "run of the herd" or a carefully selected group. In the latter case, we will put little or no faith in the index.

Practical Shortcomings of the Progeny Test.—It seems evident from the foregoing study that the progeny test of a breeding animal is in a very different category from the type test and the current-pedigree test. By means of the progeny test we can, it would seem, get a fairly definite idea as to the transmitting ability of a bull from a production standpoint. However, some practical considerations would indicate that even this method of breeding with bulls which have been tested by the progeny method and found desirable has serious shortcomings. In the first place, the method is expensive, because it implies the using of a one- or two-year-old bull on 12 or 15 cows and then setting the bull aside for a period of years and waiting to see how his daughters' milk yield compares with that of their dams. The gestation period in cattle is 9 months. The heifers are not bred until they are eighteen months old, then follows their gestation period of 9 months, and finally they must go through a 10 months' lactation period. This is a total of 48 months, or 4 years, which must elapse after a bull reaches sexual maturity until his genetic make-up can be learned. Quite obviously such a procedure would

never be put into practice except by an infinitesimally small number of the most affluent and farsighted breeders. In addition to the time and financial aspects involved in such a system of breeding only from proved sires, there is the additional fact that only a relatively small percentage of bulls would be proved good in any event.

Several state-wide inquiries in the United States have revealed that the average age of dairy bulls in service is about 2½ to 3½ years. Many

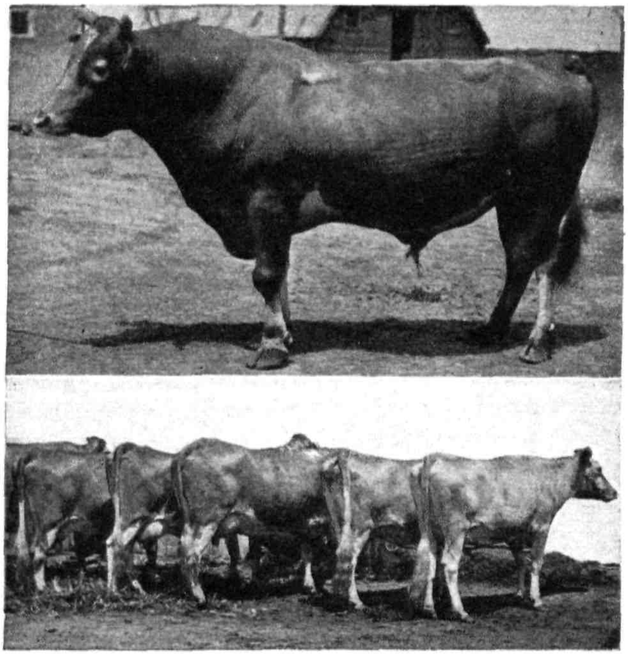

FIG. 170.—A proved Guernsey bull and some of his daughters. Ten dams averaged 333 lb. of fat; 10 daughters averaged 533 lb. of fat. *(Courtesy of W. D. Hoard & Sons Publishing Co.)*

dairymen will not keep an old bull because (1) of the danger involved, (2) of a wish to avoid inbreeding, and (3) of the danger of sterility.

Lush and Lacy have analyzed this problem in a very thoroughgoing way as the following quotation will indicate.

Table 50 shows an estimate of the age distribution which might be expected among dairy bulls if the value of proven sires were so thoroughly appreciated that every bull thought worth using in the first place was kept (unless natural causes of death or sterility interfered) until he could be proven and if all those proven to be distinctly better than the average of their breed were kept after the proving as long as they remained fertile and healthy. The figures in the table represent the maximum which could be attained in the direction of using as many proved sires as possible for dairy breeding. There are several rough approxi-

mations in the table as for instance the estimate that during the first five years the losses from sterility and death from natural causes would only be a little more than 2.5 per cent per year and that after the bulls had passed 8 years the losses from the same causes would run some 13 per cent per year and higher.

If these estimates are roughly correct, for every 1,000 bulls thought worth trying as sires in the first place, approximately 900 would go past 5 years of age and begin to be proven by the records of their daughters. Extensive data already collected[1] upon proven sires indicate that about one-third actually lower the production of the herds in which they are used, another third do not change the production much one way or the other and one-third produce distinct increases in the production of the herds where they are used. Therefore it is likely that of the 900 bulls which begin to be proven between 5 and 6 years of age it would rather quickly become apparent that about 300 of them were below the average

Table 50.—Age Distribution of Dairy Sires Attainable If All Possible Efforts Were Made to Prove Sires and to Use as Long as Possible Those Proved Good

Steps in the proving process	Age of sire	Number of sires alive at this age	Number of sires that go out of service during year	Reason for decrease
5-year period before the daughters begin to prove the sires	1	1,000	...	Deaths and sterility from disease and accident
	2	975	25	
	3	950	25	
	4	925	25	
	5	900	25	
3-year period when proof is coming in and being culled accordingly	6	600	300	Disease and accident plus the culling of ⅓ which prove to be distinctly inferior
	7	450	150	Further culling of ½ those proved mediocre
	8	300	150	Culling of the remaining mediocre ones
Period after proof is complete and only the distinctly superior sires are kept	9	260	40	Deaths and sterility from disease and accident
	10	220	40	
	11	180	40	
	12	145	35	
	13	110	35	
	14	75	35	
	15	40	35	
	16	15	25	

[1] McDowell, J. C., and Wintermeyer, W. E., Proved Dairy Sires, *U.S. Dept. Agr. Cir.* 3, September, 1927.

merit of their breed and these would be discarded promptly. Of course the evidence would not all be available at once, and there would be many bulls about which the breeder would still be in doubt when they were 6 or 7 years of age. In the table it is indicated that about half of the medium bulls would have their mediocrity definitely enough proven so that they would be discarded between the ages of 6 and 7 and the remaining half would be discarded the following year.

This would leave about 300 bulls which would be proven to be good and would still be alive at 8 years of age so that they would be available for further use. An annual loss of 30 or 40 each year through death and sterility from causes not under the breeder's control (only an estimate but probably not unduly high) furnishes the basis for the remaining figures in Table 50. When the figures in Table 50 are added it is seen that there would be at any one time only 1,345 bulls 8 years of age or older which would be clearly proven to be superior sires among a total of 7,145 in use. This is not quite 20 per cent of the entire number of bulls in service. One thousand fifty more (those between 6 and 8 years of age) would be in the process of being proven and the very poorest sires would all have been discarded from this group. This would make a total under such nearly ideal conditions of about one-third of the sires in actual use which are either proven to be good or are partially proven and are indicated to be at least of average merit.[1]

It becomes apparent, therefore, that, although the only method so far proposed for ascertaining the transmitting abilities of our dairy cattle, bulls especially, is scientifically sound, it has very practical limitations as far as expediting the creation of a more beautiful and more efficient population of dairy cows.

Formulation of the Pedigree Index.—Realizing that good proved bulls are scarce and costly and that for many years to come most of our dairy-cattle breeders will still be using young bulls, the writer has attempted to develop a method whereby the transmitting ability of a bull calf, as far as amount of milk and percentage of fat are concerned, might be fairly accurately ascertained.

An example of the workings of this system is afforded in the three Guernsey bulls Langwater Knight, Langwater Valiant, and Langwater Mixter (Fig. 171). These bulls are full brothers, all of them being by Langwater Warrior and out of Langwater Generous. The question is whether or not, by utilizing all the production records of the animals occurring in the first two generations of these bulls' pedigrees, we might be able to devise a formula that will tell us the approximate genetic make-up of these bulls for amount of milk and percentage of fat.

We can, of course, find the indexes of the sire and the two grandsires. For example, Langwater Warrior was bred to 30 cows whose average production was 15,418 lb. of 4.85 per cent milk. The resulting 30 daughters averaged 14,250 lb. of 4.86 per cent milk, thus giving Lang-

[1] Lush, J. L., and Lacy, M. D., The Ages of Breeding Cattle and the Possibility of Having Proved Sires, *Iowa Agr. Expt. Sta. Bul.* 290, 1932.

water Warrior an intermediate index of 13,082 lb. of 4.87 per cent milk, as indicated in Fig. 171. The fraction to the left of Langwater Warrior's index in Fig. 171 indicates by the numerator the number of daughter-dam comparisons available for use in figuring his index and by the denominator the number of registered daughters that he sired. The fraction to the right of Langwater Warrior's index indicates by the numerator the percentage of his daughters that exceeded their dams in amount of milk and by the denominator the percentage of his daughters that exceeded their dams in fat percentage. The two grandsires in Fig. 171 are figured in a similar manner.

Now, when we come to the cows in the pedigree of these three full brothers, we are anxious to get all of the information possible. We know from experience that a cow's record is not a very safe criterion of her genetic make-up. We should use the cow's record, however, together with other useful information. In the case of Langwater Lily (the paternal granddam), for example, we can include the sire's index and in this way include all of her half sisters by the same sire. We find also that Langwater Lily had 3 daughters with records. These 3 daughters' records averaged 15,241 lb. of 5.20 per cent milk, whereas their 3 sires' indexes averaged 15,263 lb. of 5.25 per cent milk. From these figures we can secure an index of this cow, Langwater Lily, based upon what she evidently transmitted to her daughters. By the use of the intermediate system, her index based on these 3 daughters was 15,219 lb. of 5.15 per cent milk. Langwater Lily also had 4 sons whose average index was found to be 12,790 lb. of 5.21 per cent milk, whereas their 4 sires' indexes averaged 14,480 lb. of 5.38 per cent milk. It is evident, therefore, that the cow Langwater Lily must have contributed on the average 11,100 lb. of 5.04 per cent milk to these 4 sons, and this latter figure is her index based on the performance of her 4 sons. We now have for Langwater Lily four lines of evidence bearing on her genetic make-up for amount of milk and percentage of fat:

Pounds of Milk	Percentage of Fat
10,290	5.33 (her own record)
12,342	5.39 (her sire's index)
15,219	5.15 (her index based on 3 daughters)
11,100	5.04 (her index based on 4 sons)

The average of these four figures is 12,240 lb. of 5.23 per cent milk, and we shall use this as the probable transmitting ability of this cow. The transmitting index of Florham Pride was secured in the same manner. The transmitting index of Langwater Generous was also secured this way, except that her index was not figured on her sons because these are the animals we are studying.

Langwater Knight: 13 daughter-dam comparisons
15,322 4.80 Cows bred to average
14,169 5.00 Pedigree index
29,491 9.80
14,745 4.90 Daughters should have done
15,694 4.88 Daughters did (error 6.2%)

Langwater Valiant: 10 daughter-dam comparisons
14,662 4.89 Cows bred to average
14,169 5.00 Pedigree index
28,831 9.89
14,415 4.94 Daughters should have done
14,949 4.89 Daughters did (error 3.0%)

Langwater Mixter: 13 daughter-dam comparisons
14,454 5.45 Cows bred to average
14,169 5.00 Pedigree index
28,623 10.45
14,311 5.22 Daughters should have done
12,458 4.87 Daughters did (error 16.8%)

Pedigree index
14,170 5.00

Langwater Warrior:
$\frac{30}{74}$ 13,082 4.87 $\frac{33}{37}$+

King of the May:
$\frac{21}{52}$ 16,202 5.16 $\frac{76}{52}$

Langwater Lily:
Her record 10,290 5.33
Sire's index 12,342 5.39
Her index (3 daughters) 15,219 5.15
Her index (4 sons) 11,100 5.04
Transmitting index 12,240 5.23

Golden Secret:
3 daughters' average 15,241 5.20
3 sires' index average 15,263 5.25
4 sons' index average 12,790 5.21
4 sires' index average 14,480 5.38

Langwater Generous:
Her record 14,792 4.97
Sire's index 16,202 5.16
Her index (3 daughters) 13,758 4.86
Transmitting index 14,917 4.99
3 daughters' average 13,938 5.15
3 sires' average 14,118 5.44

King of the May:
$\frac{21}{52}$ 16,202 5.16 $\frac{76}{52}$+

Florham Pride:
Her record 13,352 4.69
Sire's index 14,209 5.14
Her index (2 daughters) 16,829 4.75
Her index (2 sons) 7,777 5.13
Transmitting index 13,042 4.93

May Rose King:
2 daughters' average 15,563 4.77
2 sires' index average 14,397 4.79
2 sons' index average 10,245 4.75
2 sires' index average 12,713 4.37

FIG. 171.—Genetic study of three full brothers.

We now have indexes on the sire and dam and also on the two grandsires and granddams. The question is how to put these together to get at what the sons of Generous by Warrior are likely to transmit. Theoretically we should let the parental generation count for one-half, the grandparental for one-fourth, etc. However, we have only two generations complete. What was done, therefore, was to add the sire's index and the dam's index together, divide by 2 to get the average for parental generation.

13,082	4.87
14,917	4.99
2/27,999	2/9.86
13,999	4.93

In like manner to get the average for the grandparental generation:

16,202	5.16
12,240	5.23
16,202	5.16
13,042	4.93
4/57,686	/20.48
14,421	5.12

Now in order to make the first or parental generation of a little greater importance than the second, we take 0.6 of

13,999	4.93
0.6	0.6
8,399.4	2.958

and 0.4 of

14,221	5.12
0.4	0.4
5,768.4	2.048

and add

8,339.4	2.958
14,167.8	5.006

and to put it in round numbers we have 14,170 lb. milk and 5.00 per cent as the theoretical transmitting ability of these three full brothers, and the writer would suggest that this be called a *pedigree index*.

Now we can test this pedigree index and find out how accurate it is for these three full brothers. As indicated in Fig. 171, Langwater Knight was bred to 13 cows whose average production was 15,322 lb. of 4.80 per cent milk. If the figure 14,170 lb. of 5.00 per cent milk is correct for this bull, then the 13 daughters should have produced 14,745 lb. of 4.90

per cent milk. Their records show, however, that they actually did produce 15,694 lb. of 4.88 per cent milk. They yielded a little more milk of a slightly lower fat content than we expected. According to Gaines and Davidson's formula, 14,745 lb. of 4.90 per cent milk is the equivalent of 16,728 lb. of 4 per cent fat-corrected milk. (To reduce milk of any fat content to a standard 4 per cent fat-corrected milk basis, take 0.4 of the milk and add to it 15 times the fat, *i.e.*, total fat.) In like manner 15,694 lb. of 4.88 per cent milk is equivalent to 17,767 lb. of 4 per cent fat-corrected milk. These 13 daughters, therefore, produced 1,039 lb. of 4 per cent fat-corrected milk more than we expected; *i.e.*, they exceeded expectations by 6.2 per cent. Figure 171 shows that the 10 daughters of Langwater Valiant exceeded expectations by 3.0 per cent, whereas the daughters of Langwater Mixter failed to come up to expectations by 16.8 per cent.

It is, of course, possible that the daughters of Langwater Mixter did not have so good an opportunity as did those of Knight and Valiant. We do know that, speaking generally, the daughters of a bull are tested under the same general conditions and usually on the same farm where their dams were tested.

The writer believes that the procedure as outlined herewith will tell us the best that we can expect from a young bull. It cannot be perfect, for the simple reason that the pedigree is not complete in terms of records, as well as because of the great probability that our dairy-cattle population will be relatively heterozygous for many years to come. For instance, in the case of Langwater Knight we have comparisons of 13 daughters with their dams out of a total of 43 registered daughters *i.e.*, the material is highly selected. The system will evidently tell us the best that we can expect, because the best records are included in the pedigree. It will not tell us the worst we can expect, because the worst records are not included in the pedigree.

When the pedigree is made complete, *i.e.*, when records are available on practically all the daughters of a bull and also on the dams of these daughters, and assuming that both the dams and their daughters are tested under similar conditions, then one will be able to make a more accurate prediction.

Figure 172 gives the results of a genetic study of the two full brothers Winterthur Bess Ormsby Boast and Winterthur Bess Ormsby Great, the former showing a 2 per cent error on 25 daughters and the latter an 8 per cent error on 6 daughters.

The writer has worked out 24 bulls from among the Holstein, Guernsey, and Jersey breeds, and the average error through the use of pedigree indexes turned out to be 5.3 per cent on an average of 19 daughters per bull. In other words, by means of the pedigree index we could

have predicted, the day these bulls were born, to within 5.3 per cent how much their daughters would produce on the average if we knew the average production of the cows in the herds in which they were to be used. This is the way in which the pedigree index would be used in actual practice.

The writer has indicated previously that the Advanced Registry records cannot at present tell the whole story because of their incompleteness. For example, a bull may have 60 registered daughters but only 20 on which daughter-dam comparisons are possible. These are

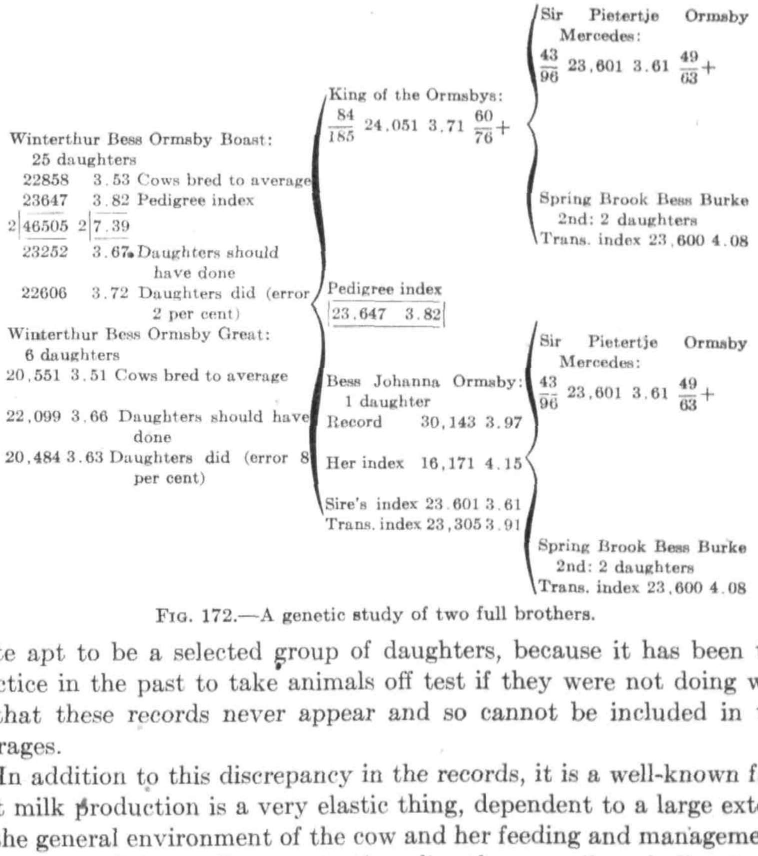

FIG. 172.—A genetic study of two full brothers.

quite apt to be a selected group of daughters, because it has been the practice in the past to take animals off test if they were not doing well so that these records never appear and so cannot be included in the averages.

In addition to this discrepancy in the records, it is a well-known fact that milk production is a very elastic thing, dependent to a large extent on the general environment of the cow and her feeding and management. Weather conditions affect production directly as well as indirectly in the type of feed produced in different years. The daughters of a bull may be tested under extremely favorable or unfavorable conditions as compared with the dams of said daughters. These points have been advocated quite strongly by certain breeders who are antagonistic to indexing bulls. It certainly provides an excellent smoke screen behind

which those can hide who do not wish the truth concerning their animals brought out into the open. Dealing with such a complex biological and physiological process as milk production, one cannot or should not hope for absolute accuracy, but a system correct to within 5 to 10 per cent should have, it would seem, great utility.

Use of the Pedigree Index as a Tool in the Selection of Dairy Cattle.—In order to give an example as to how a breeder might use a pedigree index, the writer has computed such an index for the present Holstein herd sire at the Massachusetts State College, *viz.*, Dad Ormsby Jupiter (Fig. 173). This is a young bull, five and a half years of age, and as

Dad Ormsby Jupiter, 571003:
22815 3.43 Cow's average M.S.C.
22649 3.65 Pedigree index
2|45464| |7.08|
22732 3.54 Daughters will average

Jemima Riverside Boast Ormsby Dad:
$\frac{21}{?}$ 21138 3.65 $\frac{48}{55}$+

Pedigree index
|22,649 M. 3.65 F.|

Winterthur Ormsby Deresa:
Her record 24,238 3.50
Trans. index 24,144 3.60

Winterthur Bess Ormsby Boast:
$\frac{22}{40}$ 22,352 3.91 $\frac{44}{75}$+

Llenroc Johanna Rue Alice:
Her record 23,173 4.07
Trans. index 22,806 3.76

King of the Ormsbys:
$\frac{84}{185}$ 24 050 3.71 $\frac{60}{76}$+

Vanderkamp Segis Teresa (1 daughter):
Her record 20,468 3.37
Trans. index 21,422 3.42

FIG. 173.—A pedigree index of a young Holstein herd sire at Massachusetts State College.

yet he has no daughters that have completed records. We, of course, are curious to know what we can expect in the way of production from this bull, and we believe that we can get a pretty fair notion from his pedigree index. In Fig. 173 will be found the pedigree of this bull and his computed pedigree index. We have in the college herd at this time 17 cows that have completed records, and these records average 22,815 lb. milk testing 3.43 per cent. Now, based on the pedigree index of Dad Ormsby Jupiter, 22,649 lb. of milk testing 3.65 per cent, we expect the daughters of this bull out of our cows to average about halfway between the cow's level of production and the bull's pedigree index:

22,815	3.43
22,649	3.65
2/45,464	7.08
22,732	3.54

The expected production of the daughters of Dad Ormsby Jupiter in the Massachusetts State College herd is, therefore, 22,732 lb. of milk testing 3.54 per cent. We put the figure halfway between the dam's level and the sire's computed index because we feel that the bull and the cow are jointly and equally responsible for the average production of all their offspring. Time alone can tell how accurate our prediction turns out to be.

Getting a pedigree index on a bull from a complete two-generation pedigree certainly should make the task of selecting a herd sire (from a

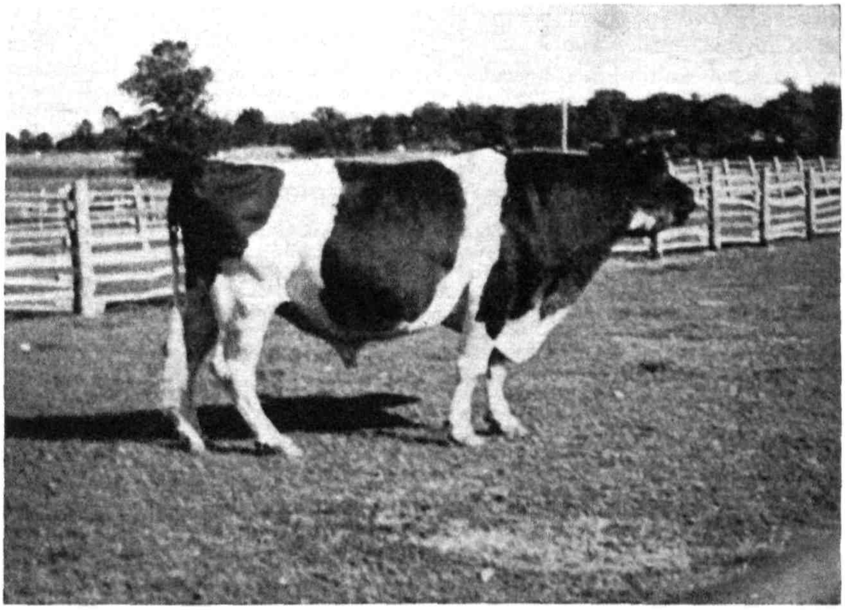

FIG. 174.—Holstein bull Dad Ormsby Jupiter.

production standpoint) very much more simple. For example, if our herd here at the college averaged 26,000 lb. of 3.70 per cent milk, we should not want to use this bull. On the other hand, if our herd average was 18,000 lb. of 3.2 per cent milk, such a bull would be very valuable. In other words, the cash value of a bull depends on the kind of cows to which he is to be mated. The bull might be worth less than nothing in some herds and worth thousands of dollars in others.

The above was written in 1934. It is now 1941, and we can check the accuracy of our prediction for the bull Dad Ormsby Jupiter. In the Massachusetts State College herd, Dad has been bred to 15 cows whose average production was 19,035 lb. of milk with a 3.65 per cent test. We

would expect the daughters to produce halfway between the cows' level of production and the bull's prediction or pedigree index.

19,035	3.65% test
22,649	3.65
2/41,684	2/7.30
20,842	3.65% test or 760 lb. butterfat

The 15 daughters actually have averaged 22,209 lb. of milk with a 3.42 per cent test or 760 lb. butterfat.

This bull evidently transmitted about as we figured he would from the records of his direct and collateral relatives. True, he transmitted at a higher total amount of milk and at a lower butterfat test than his pedigree would have indicated, but we must remember that pedigrees involving Advanced Registry tests cannot be made complete, for testing under this plan is optional as far as any animal is concerned with the result that only a few selected daughters of most bulls are ever tested.

Some people have the mistaken notion that indexing bulls will be a panacea for all of our breeding ills, that the breeder will no longer have to use his common sense and intelligence. This is far from correct. Owning one or more good bulls makes the job of breeding even more difficult, for, besides production probabilities both as to amount of milk and percentage of fat revealed by the pedigree index, the owners of such bulls have still the matters of type of their ancestors as well as of their daughters, mammary development, resistance to disease, persistency, ease of milking, color of the product, softness of curd, efficiency of production, etc. to consider. The daughters of some bulls, no doubt, will excel in certain of these characteristics; daughters of other bulls will excel in other respects. So there is an excellent opportunity, in fact a need, on the part of the owners of good bulls—proved good by their records—to use their skill and intelligence in breeding. To create animals not only capable of producing large amounts of high-quality product but of good type as well should, in the writer's opinion, be the aim of every breeder of dairy cattle, for although, as yet, there has been found no proof that good type necessarily means good production, neither is there any indication that good type and high production of a quality product cannot go hand in hand.

It would, therefore, seem safe to say that the indexing of bulls and of cows has a very definite and very practical value for anyone who is really interested in breeding better dairy cattle. By means of indexing, we can get a pedigree index and thus take some of the "guess" out of breeding and build our breeding operation on a firm genetic basis.

In the selection of a young bull, his pedigree index can serve as a very useful criterion of his transmitting ability for amount of milk and per-

Ear Tag No. 1159
Bull Calf
Born June 10, 1933
Pedigree Index 14,100 5.39

Foremost's Bell
Buoy, young bull, no daughters with records
13,500 5.39 Pedigree index

Langwater Foremost
Index $\frac{31}{101}$ 13,598 5.40 $\frac{54}{67}+$

Langwater Fashion
Index $\frac{9}{25}$ 12,297 5.52 $\frac{44}{90}+$

Langwater Monarch
Index 17,470 4.68
L. Pauline (no daughters)
Trans. index 14,651 5.30

Langwater Generous
Trans. Index 14,917 4.99

King of the May
Index 16,202 5.16
Florham Pride (no daughters)
Trans. index 14,797 4.86

Bell Buoy's Violet of City View
Her record 17,234 5.56
Sire's index 13,335 5.22
Her index 11,400 5.98
Trans. index 13,989 5.59

Bell Buoy of L.V.
Index $\frac{25}{58}$ 13,335 5.22 $\frac{72}{52}+$

Jethro's May King of L. V.
Index 14,730 4.72
Easton Belle (3 daughters)
Trans. index 12,488 4.46

Benton Harbor's Violet
Trans. index 11,608 5.23

Benton Harbor
Index 10,002 4.61
Lady Violet of the Isle
Imp. (1 daughter)
Her daughter's record 10,007 5.60 (no record, no sire's index)

Valor's Faithful
Young cow, no record, 14,381 5.35 Pedigree index

Langwater Valor
Index $\frac{14}{30}$ 15,654 4.89 $\frac{50}{43}+$

Langwater Valiant
Index $\frac{10}{37}$ 15,232 4.89 $\frac{50}{50}+$

Langwater Warrior
Index 13,082 4.87
L. Generous (3 daughters)
Trans. index 14,917 4.99

Langwater Queen of the East
Trans. index 13,688 5.26

Langwater Warrior
Index 13,082 4.87
L. Cleopatra (1 daughter)
Trans. index 13,688 5.26

Mixter Faithful
Her record 15,751 5.91
Sire's index 12,845 5.82
Her index 13,726 5.79
Trans. index 14,107 5.84

Langwater Demonstrator
Index $\frac{52}{168}$ 12,845 5.82 $\frac{70}{86}+$

Dolly Dimples M.K. of L.
Index 11,654 5.57
Hayes Felois 2d (3 daughters)
Trans. index 9,127 5.42

Mixter Faith
Trans. index 12,769 5.39

Duke of Waumesit
Index 11,782 5.38
30,841 (2 daughters)
Trans. index 12,624 4.92

FIG. 175.—Pedigree of a bull used for a production-transmitting estimate.

centage of fat. The pedigree index should also be used in conjunction with the performance index up until the time that the performance index is based on 10 daughter-dam pairs. When comparisons are available on 10 or more daughter-dam comparisons (unselected), the use of the pedigree index can be discontinued and the performance index used alone.

The objection to the pedigree indexing method might conceivably be raised that it is of no use in the case of a bull calf that is sired by a young bull, one without tested daughters or out of a young cow. In order to anticipate this criticism, the writer has worked out the pedigree index of such a bull calf born at Emmadine Farm, Hopewell Junction, N.Y., on June 10, 1933 (Fig. 176). This calf was sired by a young bull with as yet no tested daughters and was the first calf of a heifer. The procedure adopted was that of figuring a pedigree index on the calf's sire, Foremost's Bell Buoy, and also a pedigree index on his dam, Valor's Faithful. This was done in the usual manner by getting performance indexes on both the parental and grandparental generations of these animals and then taking 0.6 of the average of the parents' indexes plus 0.4 of the average of the grandparents' indexes as the pedigree indexes of these two animals. Then to get the pedigree index on the bull calf, 0.6 of the average of the pedigree indexes of his sire and dam was added to 0.4 of the average performance indexes of his four grandparents. These results are shown in Fig. 175.

There is a total of 2,580 records (1,446 different records) included in this compilation. It includes every daughter-dam comparison available for four generations plus the records on the sires of the dams occurring in the fourth generation. The intermediate system of indexing was used throughout. True, the records in the pedigree are not complete, but by this method one can at least learn the best that can be expected from this bull calf. Furthermore, if the average production of the cows in the herd in which he is to be used is known, a fairly accurate prediction can be made of the probable production of his future daughters.

The above was written in 1934. The work was done at the request of the late Jimmie Dodge, at that time manager of Emmadine Farm, Hopewell Junction, N.Y., with the stipulation that the writer be allowed to name the bull. The name chosen was Foremost Prediction 212227, and this is the bull whose pedigree is shown in Fig. 175.

Foremost Prediction is now eight years old and has been used at McDonald Farms, Cortland, N.Y. An inquiry addressed to the Guernsey Sire Evaluation Service at Madison, Wis., reveals the fact that Foremost Prediction now has 31 daughter-dam comparisons. We would expect that his daughters would fall halfway between his pedigree index and the average production of the cows to which he was mated.

Foremost Prediction pedigree index......	14,100	5.39% test
Cows bred to average production........	13,113	4.98% test
	2/27,213	2/10.37
Daughters should average..............	13,606	5.18% test
31 daughters do average................	13,595	5.10% test

The writer is under no illusions in regard to his ability as a prophet. The closeness of the performance to the prediction both for the Holstein bull Dad Ormsby Jupiter and Foremost Prediction was probably in large measure a matter of good fortune. Nevertheless, we are still

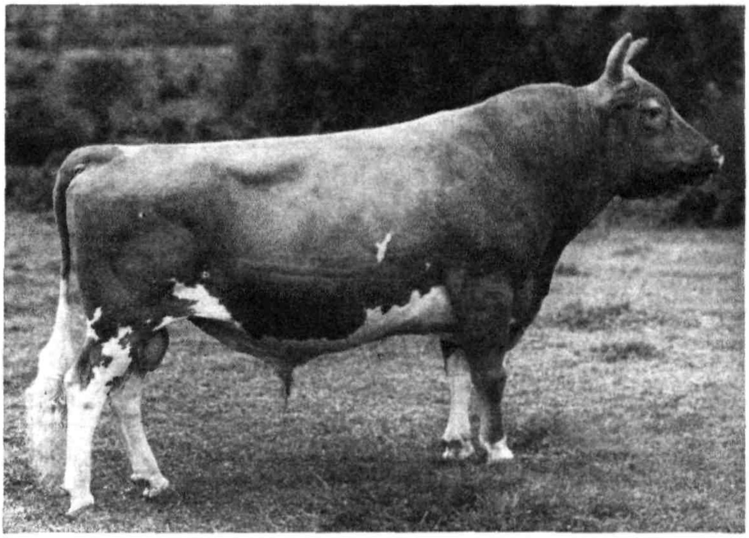

FIG. 176.—The Guernsey bull Foremost Prediction bred by Emmadine Farms, Hopewell Junction, N.Y., owned by McDonald Farms, Cortland, N.Y. (*Photograph Courtesy of Strohmeyer and Carpenter.*)

of the opinion that a pedigree made fairly complete in terms of performance can serve a very useful and generally fairly accurate estimate of the transmitting ability of any animal.

The greatest need in the breeding of dairy cattle, as stated earlier, is a selection index based on sound scientific fact to replace or rather to succor the traditional indexes of type and pedigree. To fill this need the author has suggested the pedigree index, which portrays the genetic make-up of both bulls and cows from a production standpoint in so far as the records make this possible. When records become available on all or practically all of the mates as well as the daughters of our dairy bulls, the pedigree index should prove to be a very useful selection tool in the hands of intelligent breeders.

Bull Transmitting Chart.—The art of animal photography has mad rapid progress during the last 20 or 30 years. To bring out photo graphically the best points of an animal and to minimize the weake ones is a very difficult procedure and one requiring an infinite amount o patience and practice. When the job has been well done, howeve it has decided limitations from a breeding or selection standpoint because the photograph portrays only the phenotypic aspects of th animal. In addition, the breeder also needs some method of getting picture of the animal that will portray his or her genotypic aspects.

The following graphs are an attempt to supply this need, especiall for dairy bulls. Figure 177 shows a graph for the Holstein bull, Kin of the Ormsbys, in regard to amount of milk. The 84 cows to whic this bull was mated were grouped ac cording to production to the neares 1,000 lb. The solid line of the grap (Fig. 177) shows that there was on cow in the 12,000-lb. class, one in th 13,000-lb. class, two in the 14,000-lb class, three in the 15,000-lb. class, etc The broken line of the graph show that out of these 84 cows this bul sired 3 daughters in the 15,000-lb class, 3 daughters in the 17,000-lb class, 5 in the 18,000-lb. class, etc. The dams' mean was 20,547 lb. and the daughters' mean 22,190 lb. Th standard deviation of the dams wa 3,858 lb. and that of the daughter 3,465 lb., and the coefficient of variation of the dams was 18.8 per cent and the daughters 15.6 per cent.

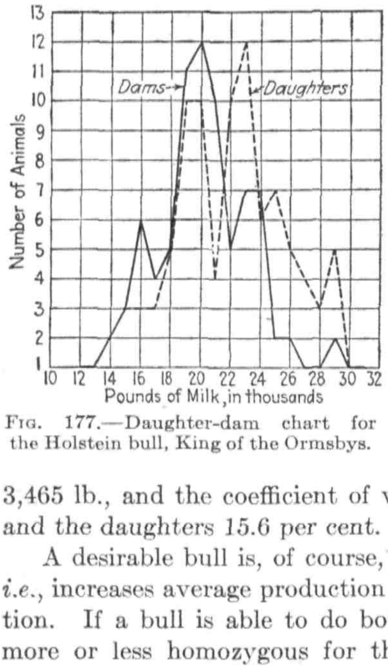

FIG. 177.—Daughter-dam chart for the Holstein bull, King of the Ormsbys.

A desirable bull is, of course, one who moves the mean to the right, *i.e.*, increases average production and also lowers the coefficient of variation. If a bull is able to do both these things, it indicates that he is more or less homozygous for the genes making for high production. This sort of graph, in other words, presents a picture of the genotypic make-up of this bull, which shows at a glance just what sort of breeder he is.

Figure 178A shows in the same manner the genotypic make-up of this bull from the standpoint of fat percentage. In this case the dams' mean was 3.34 per cent, their standard deviation was 0.288 per cent, and their coefficient of variation 8.62 per cent. The daughters' mean was 3.54 per cent, their standard deviation was 0.256 per cent, and their coefficient of variation 7.23 per cent.

Figure 178B shows a graph for this same bull on the basis of 4 per cent fat-corrected milk. The coefficient of correlation between dams' and daughters' production on a 4 per cent fat-corrected milk basis was also calculated and found to be a positive correlation of 0.57 ± 0.04, indicating that the level of production of these dams did influence considerably the level of production of their daughters, which adds weight to the argument for using both dams' and daughters' records in computing indexes for bulls.

Selecting the Heifers to Save.—For the man breeding his own replacements, there is in addition to the problem of selecting bulls, the further

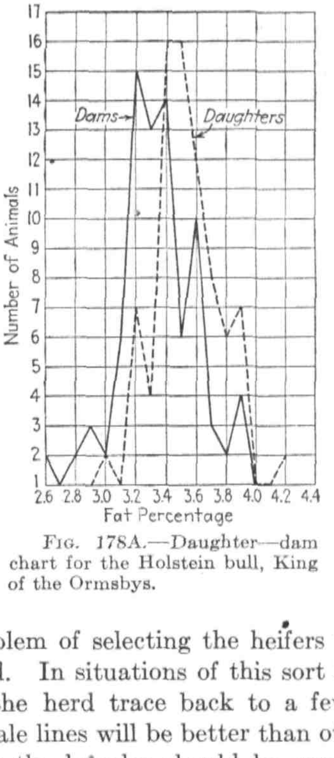

FIG. 178A.—Daughter—dam chart for the Holstein bull, King of the Ormsbys.

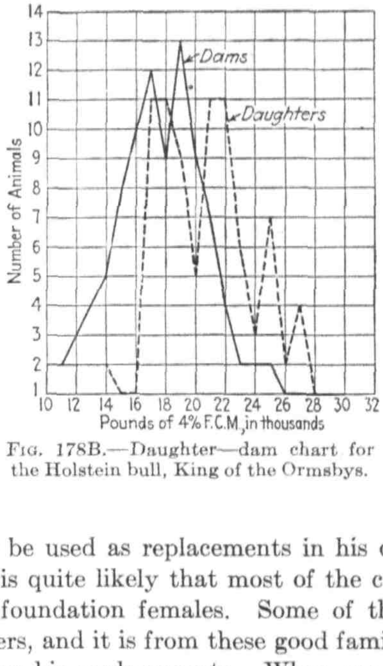

FIG. 178B.—Daughter—dam chart for the Holstein bull, King of the Ormsbys.

problem of selecting the heifers to be used as replacements in his own herd. In situations of this sort it is quite likely that most of the cows in the herd trace back to a few foundation females. Some of these female lines will be better than others, and it is from these good families that the breeder should be growing his replacements. When records have been kept for a few years, it will be possible to set the whole herd up graphically as is illustrated in Fig. 179; and, when this can be done, the breeder can eliminate a consideration of the retention of certain calves as replacements even before they are born, because they are in poor families which it is planned to eliminate gradually from his herd. Then he can devote his whole attention to choosing the better calves in the better families to serve as replacements.

Likewise the task of choosing a bull calf from another breeder's herd will be greatly simplified when the breeder can display a chart of his whole herd as indicated in Fig. 179. We may hear of a breeder with a good proved bull and decide we would like a son of this bull. We go to this farm and study the female lines as charted and try to pick our bull calf from a good female line, one in which each generation of females has proved to be better than the dams. We find from the chart two or three cows meeting this requirement, and then we go out to the barn to make our choice between these calves on the basis of their own and their

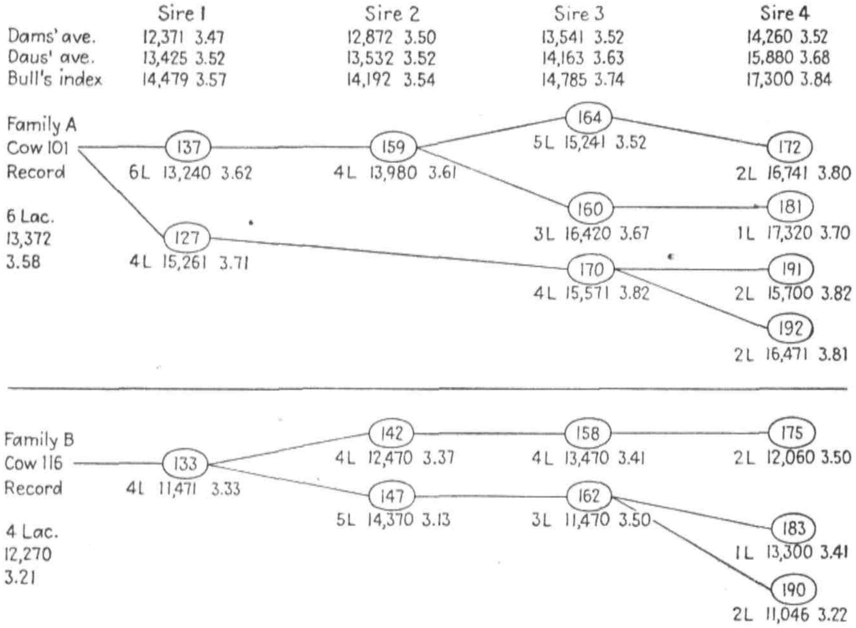

FIG. 179.—Two cow families of very different breeding worth.

close relatives' individualities. Such a scheme of selection gives a double check. We not only get a son of a good proved bull, but we secure him from a line of females that has shown steady progress generation by generation.

Two cow families are shown in Fig. 179. Family A is a good one, family B not so good. The chart is to be read in the following manner. Foundation cow 101 had 2 daughters by sire 1; one (137) averaged in 6 lactations 13,240 lb. of milk testing 3.62; the other (127) averaged 15,261 lb. of milk testing 3.71 in four lactations. In family B, foundation cow 116 had a daughter by sire 1 that averaged in four lactations 11,431 lb. of milk testing 3.33. The daughter 137 of foundation cow 101 by sire 1 in turn left a daughter (159) by sire 2 that averaged in four

lactations 13,980 lb. of milk testing 3.61; whereas the daughter (133) *of foundation cow 116 by sire 1 left 2 daughters by sire 2*, one of which averaged in four lactations 12,470 lb. of milk testing 3.37; and the other (147) averaged in five lactations 14,370 lb. of milk testing 3.13, etc.,

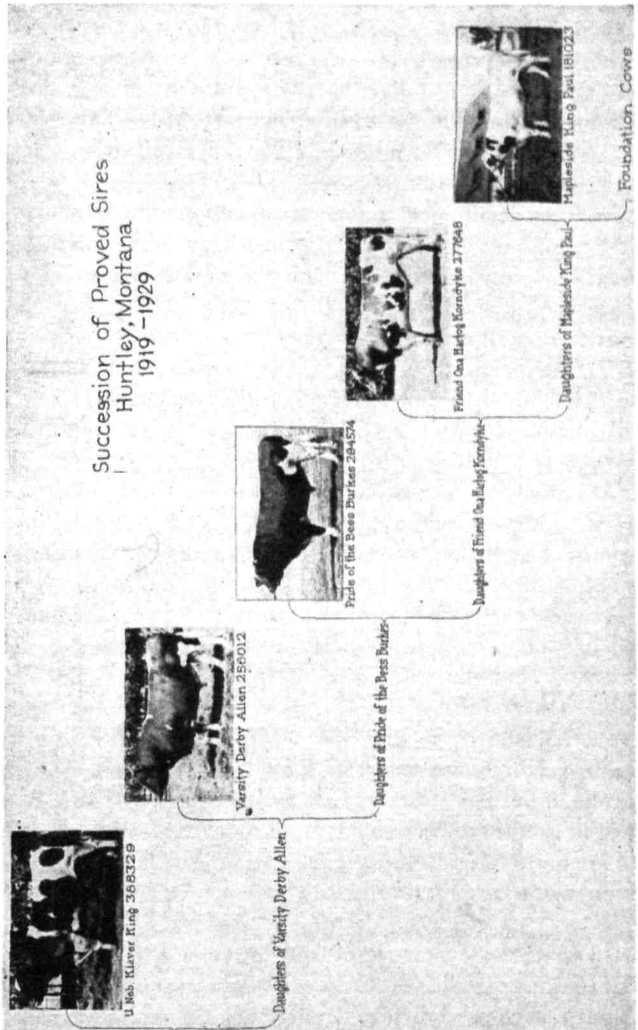

FIG. 180.—This succession of proved sires increased milk from 16,803 to 20,870 lb. and fat test from 3.44 to 3.84 per cent. (*Courtesy of Bureau of Dairy Industry, U.S. Department of Agriculture.*)

through the rest of the chart. All the descendants of foundation cow 101 (there were 20 in all) averaged to produce 16,020 lb. of milk testing 3.75 and all the descendants of foundation cow 116 (13 in all) averaged to produce 12,340 lb. of milk testing 3.34 per cent.

It is obvious that selection in family B should be stopped and selection of replacements confined to family A, with due attention given to type, longevity, ease of milking, freedom from disease, etc. If a breeder keeps records, he can analyze his herd in the above fashion, and only then is he in a position to select his female replacements intelligently. If he does this and uses care in the selection of his sires, there is no reason why he cannot make progress in building up a higher producing herd. Records provide the only intelligent basis for the art of selection.

Other Considerations in Selecting Dairy Cattle.—There are many other considerations to be borne in mind in selecting dairy cattle, only a few of which will be mentioned here.

From a practical standpoint a dairyman desires to have a herd of cows that are not too high-strung and nervous, are easy milkers either at hand or machine milking, and have teats which are neither too large nor too small and are well-placed on the udder. He also desires cows that calve easily and without complications and those not particularly subject to going off feed or prone to develop udder troubles such as leaky teats, mastitis, etc. He hopes to develop a generally vigorous strain of animals and a strain that maintains high production for a long time during each lactation period and remains productive over a long period of years. The matter of longevity is especially important, for it takes about the first 2 years of a cow's productive life to repay the cost of growing her up to two years of age, or her cash cost if purchased. In addition, the range of selection is seriously curtailed if cows stay in the herd but a short time, in other words, the faster the rate of turnover, the less effective can selection be. To evaluate properly all the considerations that have been discussed in this chapter makes it imperative for the breeder to keep records. Many forms have been developed for this purpose, a sample of which is shown in Fig. 181. Most of the characteristics for which or against which we select in dairy cattle are the result of the combined action of heredity and environment. Only with fairly complete recorded data is the breeder enabled to discover the strains and families within his own herd that have a preponderance of the genes which he desires to increase and a minimum of those which he would like to rid himself of.

Finally, the matter of efficiency of feed conversion should receive some attention in making selections. Several investigations have demonstrated that variations in ability to convert feed in excess of maintenance requirements into milk exist among dairy cows. A study by W. T. Smith and the writer on the matter of efficiency of feed conversion among 42 cows in the Massachusetts State College Experiment Station herd in 136 lactations over a period of 13 years showed efficiencies ranging from 18.12 per cent to 39.6 per cent with an average efficiency of 29.25 per

No.________ Breed________

Record Card for Each Cow

Name________

Breeder________

Date of Birth________

Weight at Maturity________

Picture

Records

Length of Record	Number Milk-ings	Age at Start	Total Production Milk	Total Production Test	Total Production Fat	305 C Mature Milk	305 C Mature Test	305 C Mature Fat

Daughter's Records 305 C Mature

Name	No.	Milk	Test	Fat

Date Bred	Bred To	Date Calved	Length Gestation	Sex of Calf	Remarks	What became of calf

FIG. 181.—Record card for use in dairy herd (see other side).—(*Continued*).

Pedigree____________________

Grandsire ____________________

Sire ____________________

Index:

Grandam ____________________

Grandsire ____________________

Dam ____________________

Ave. Record (305 C Mature):

Grandam ____________________

Other Remarks

Type

Ease of milking

Persistency

Heat periods

Remarks:____________________

Health Record

T.B. Test____________________

C.A. Test____________________

Mastitis____________________

Other Troubles____________________

Sold at______years of age because____________

FIG. 181.—Record card for use in dairy herd (see other side).—(*Continued*)

cent. One cow put 39.6 lb. of total digestible nutrients into the milk pail for each 100 lb. of total digestible nutrients fed, another only 18.12 lb. In general, the higher producing cows were more efficient. Any cow's rate of efficiency was fairly constant at all ages, being somewhat lower of course while the animals were still growing. One bull's daughters were 5.21 per cent less efficient than their dams, another bull's daughters were 4.17 per cent more efficient than their dams. That efficiency of feed conversion has a hereditary basis seems quite likely. To measure things of this nature requires more feed weighing and record keeping than the average breeder is equipped to provide, but most breeders can point out cows in their barns that require smaller amounts of high-priced concentrates than do others for the same amount of production. The high correlation between amount of production and efficiency of feed conversion makes it likely that selection aimed at higher production will also to a considerable extent take care of the matter of efficiency of feed conversion.

Summary.—It is hoped that the discussions in this chapter have made it evident that the task of selecting dairy animals should be based quite largely on records. Records of production properly standardized can yield an index of a bull's transmitting abilities for amount of milk and butterfat test. Records on the cows in a breeder's herd can be so arranged as readily to reveal the better female lines in the herd. Records of many other qualities besides production, *e.g.*, health, disposition, type, regularity of breeding, etc., must be available if a breeder is to be eventually successful in establishing desirable qualities in and eliminating undesirable ones from his herd. When sufficient records are available in a pedigree, it would seem to be possible to predict with considerable accuracy what a projected or newborn individual can be expected to transmit.

Selection in dairy cattle is admittedly complex because many genes are involved, the environment plays such a large role, and we must necessarily select for and against many things simultaneously.

In breeding his own replacements a man should try to buy bulls whose pedigrees can be filled in with the sort of records that will give some idea as to what the bull in question may transmit to his daughters. If one cannot get a proved bull, he should at least try to get a son of a good proved bull out of a daughter of a good proved sire, and the inclusion of this daughter in a good family should receive at least as much consideration as her own record.

In the purchase of bulls one should avoid those with no tangible evidence of freedom from disease, with sufficient age to be proved but lacking proof, with "holes" in their pedigrees, with a lack of the marks of dairy quality, with some good but many poor close relatives, with

evidence of weak constitution and general lack of size, with pedigrees too incomplete in terms of proved dairy production.

In the purchase of cows, one should patronize only breeders and dealers of unquestioned integrity and never buy cows with no records of production, with no tangible evidence of freedom from disease, with meaty udders, pendulous, lumpy or broken away udders, with a lack of body capacity and udder capacity, with short necks, chunky, meaty bodies, with narrow pelvis, short, narrow, droopy rumps, with evidence of weak constitution and general lack of size, with a lot of poor close relatives.

In the purchase of heifers, one should avoid those with no tangible evidence of freedom from disease, with no prospect of a sound, large, quality udder, with a marked beefy tendency, with a marked deficiency of size for age, with a lack of proved dairy quality in their close relatives, with sire of unknown or poor dairy-transmitting qualities.

The breeder must keep production records on all the females in his herd year after year for the twofold purpose of spotting the "boarder" and of providing himself an opportunity to select wisely in his best cow families.

Our first job as animal breeders is to

Analyze. Find out what we have, and we do this by means of complete record keeping.

and second to

Synthesize. Fit together known hereditary materials in our animals into more efficient and more beautiful forms, and we do this by systems of breeding and selection.

Successful dairying depends in the final analysis on the inherent milk-producing qualities of the individual cows in the dairy herd. For efficient economical production they must be healthy and endowed by nature with the bodily mechanism and temperament that will permit them to consume large quantities of feed and to convert this feed into large quantities of high-quality milk over a long period of years. In order to ensure continuing success for the industry, breeders must contrive ways to create increasingly more efficient animals, and this is only possible through the intelligent appreciation of facts established through honest and unprejudiced record keeping.

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CHAPTER XXIV

SELECTION IN HORSES

The creation by selection of the various types of horses from one or a few wild progenitors has been one of man's most interesting and most helpful accomplishments. The development of more efficient power to accomplish physical labor is simply the story of an advancing civilization. As a savage, man's only source of power was his own muscle, and in order to survive he had to use it so continuously that little time or energy was left for cerebration. At some time the idea dawned of using animal power to supplement or replace his own limited supply, and many animals have been so used, among others the dog, ox, yak, camel, llama, goat, elephant, ass, and horse. Later, water, steam, gas, electricity, and gasoline were used, and now the search is on to discover methods of unleashing the power of the atom.

The following figures[1] suggest the very rapid rate of increase in mechanical power in the United States during the past 80 years.

Year	Total horsepower (in prime movers)	Horsepower (per capita)
1860	15,793,000	0.50
1900	64,193,000	0.90
1940	1,230,816,000*	9.35

* For tractors and automobiles drawbar equivalent was used rather than rated horsepower.

If we calculate that one horsepower is the equivalent of ten manpower, it is evident that each person living in the United States in 1940 had as his servants the equivalent of about 93 slaves. (Like the writer, you probably wish at times that some of these 93 were a little nearer at hand.)

Savages existed with no source of power save their own muscle, and without the adoption of outside sources of power we would still be eking out a precarious existence as savages.

In 1787, the year the Constitution was framed, the surplus food produced by 19 farmers went to feed one city person. In recent years 19 people on farms have produced enough food for 56 nonfarm people plus 10 living abroad.[2]

[1] Figures supplied through kindness of Z. R. Pettit, Chief Statistician for Agriculture, Bureau of the Census, Department of Commerce, Washington, D.C.

[2] McCrory, S. H., Hendrickson, R. F., and Committee, Technological Trends in Relation to Agriculture, a Reprint from Report of Subcommittee on Technology to the National Resources Committee, p. 99, 1937.

This is probably due, for the most part, to the fact that the modern farmer has more efficient sources of power. In ancient times a few people could live well and enjoy leisure because they had enslaved other human beings who were compelled to work for their keep. Today our slaves in America are machines.

Among the animals that have been domesticated and whose energy has been used to supplant human muscle, the horse is the most interesting and the most important. Next to the dog, among the larger animals, the horse apparently has the greatest capacity for responding to man's friendship. From the earliest times he was both helpmate and companion. The maximum efficiency of both man and horse during work, according to the researches of Brody and Trowbridge,[1] stands at 24 per cent, with steam engines at 15 per cent, gasoline engines at 18 per cent "at the belt" and about 13 per cent "at the drawbar," and Diesel engines at 35 per cent. Many other factors, of course, are involved in the choice of the "best" source of farm power.

In addition to supplying power the horse has filled a great variety of human needs. History, unfortunately, is too largely the story of war and conquest, and, although "struggle" is the keynote and first necessity of a nation's or an individual's progress, it is to be hoped that less devastating forms of struggle than war can speedily be devised. Associated with the famous warriors of the past, there generally is found their favorite horses, *e.g.*, Alexander the Great and Bucephalus, Napoleon and Marengo, Washington and Nelson, Grant and Jack, Lee and Traveler. These men's names live in history; their physical likenesses, generally astride their favorite horse, on canvas or in bronze. The place of cavalry in war is too well-known to need repetition here, and the same is true of the place of the horse in moving supplies, guns, and other equipment. During the First World War the United States shipped abroad for war purposes nearly 1 million horses and over ⅓ million mules. And, in spite of motorization, the horse seems to be playing practically as important a part as ever in the present war, for Germany is estimated to have used over 200,000 horses and mules in the Polish campaign and 750,000 in the conquest of the Low Countries and France.

In addition to his services in work or war the horse has filled and will probably continue to fill a great place in pleasure and sport. In colonial America, he provided the most rapid means of land transportation. The American Standardbred and Saddlebred finally grew out of this in the Southern colonies and even today Virginia, Tennessee, and Kentucky retain first place in the production of this light horse type. The Middle and Northern colonies developed a somewhat heavier

[1] Brody, S., and Trowbridge, E. A., Efficiency of Horses, Men and Motors, *Mo. Agr. Expt. Sta. Bul.* 383.

general-utility horse, which provided the basis for the later draft-horse development. Riding, racing, and polo still claim the attention of millions of Americans, and there appears to be little likelihood of abatement of this interest.

As a source of power in cities and on farms the horse is having serious competition from the gasoline engine. Both the motor and the horse have advantages, some of which are listed below.

Motor Advantages	Horse Advantages
More work in given time.	Lower initial investment and depreciation.
No permanent unsoundnesses or disease.	Power of reproducing.
Can work day and night.	Live on home-produced feeds.
No care nor fuel while not working.	Flexibility-use 1 or 30.
Less man power needed.	Help maintain soil fertility.
Use for belt power and custom work.	Less actual cash outlay.

The advantages of one are to a certain if not the full degree disadvantages of the other. Whether motors will eventually displace horses as a source of farm power is for the future to answer. The American farmer, like workers in all other fields, is becoming more and more efficient, *i.e.*, he produces more in less time and with less human physical effort. This tends to create a puzzling economic problem, for it means we cannot profitably consume all that is produced if all work as many hours a day or a week as they did under less efficient methods of production. As individuals, we are not interested in efficiency for efficiency's sake but only in translating efficiency into better living for ourselves and our families. If our efficiency can be made to mean a greater net income or the same income from less hours of labor, the average man is definitely interested. Hours of labor have shown a steady decline for the past 40 years; it is probable that the bottom has not yet been reached.

The farmer is on the lookout for more efficient sources of power. If engineers can provide machines that can do the general run of farm work more efficiently and more cheaply than can the horse, it seems certain that farmers will find ways to buy these machines. Table 51 (next page) shows something of the trend in forms of power on the farm over the past 20 years.

Whether or not this rapid adoption of mechanical power has in any given instance or in general been wise is a debatable point; in many instances it has meant increasing the farm mortgage or hanging the millstone of installment payments around the farmer's neck.

TABLE 51.—POWER ON FARMS

	1920	1930	1940
Horses and mules	25,742,000	19,124,000	13,931,000
Tractors	229,332	920,021	1,567,430
Farms with electricity	....	841,310	2,032,316
Trucks	150,000*	900,385	1,047,084
Automobiles	2,000,000*	4,134,675	4,144,136

* Estimate.

In any event the farm horse is going to have to try to meet this competition. It seems unlikely that the farm horse will be totally replaced by machines, and it is evident that horse breeders must use every possible means to improve their methods of selection so that only sound, durable, and efficient types of horses will be produced.

Many farmers who keep horses and raise colts do not have sufficient numbers of animals to justify the keeping of a stallion, which means that they must patronize various and sundry owners of stallions. In the early part of the twentieth century, there were many unsound and poor type stallions standing for public service at low rates in the Midwest, and many also that were improperly registered. In order to protect both the owners of good purebred stallions and the owners of mares, some states inaugurated stallion-enrollment registration services, which required the payment of a fee for registration provided the stallion was adjudged sound upon inspection by a veterinarian, the public display of the license, and the inclusion of a copy of the license in all advertising. Other states were, of course, forced to follow suit to prevent the dumping within their borders of poor stallions from states that had adopted such legislation. This is the only class of animals in which legislation has been invoked as an aid in bringing about improvement. Twenty-two states from New York and New Jersey on the Atlantic to Washington and Oregon on the Pacific and including New Mexico and Oklahoma in the South now have stallion registration boards, and a national association of these state boards was formed in 1910 and is still functioning with Prof. W. L. Blizzard of Oklahoma as its president and Prof. R. B. Cooley of Indiana as secretary.

Although the state laws vary somewhat, in general it may be said that to be eligible for public service (with or without a fee) a stallion must be free from sidebone, ringbone, bone spavin, curb (when accompanied by curby formation of the hock), glanders—farcy, *maladie-du-coït*, urethral gleet, and mange. He must be registered in a nationally recognized registry association or be advertised as a grade. In some states only sound purebred stallions are eligible for a license.

The main purposes of stallion-enrollment laws were and are to prevent misrepresentation in advertising and to prohibit the use of sires thought likely to spread infectious diseases or a conformation that would not stand up under hard work and conversely to encourage the development of a sound breeding program for horses. That these stallion-enrollment laws have accomplished their main purposes cannot be questioned, and, although it is impossible to estimate their financial advantages to *breeders, farmers, and the respective states, their contribution to a better* average type of horse is admittedly very great.

General Bases for Selection in Horses.—In general there are five types of horses, *viz.*, draft, heavy harness, light harness, saddlers, and ponies. They are maintained in the final analysis for but one thing, their ability to move for its own sake, as in the various types of racing, driving, hunting, riding, polo playing, etc., or their ability to move loads, as in various forms of draft work. The criterion of selection in horses has always been their ability to do certain things plus in some instances their beauty of appearance. In the heavy and light harness horses, the pony, and the saddle horse used in the show ring, perhaps equal weight has been given to appearance and performance. In the hunter, utility saddler, draft, and various types of race horses the main influence shaping selection has been performance with somewhat less attention paid to appearance. The distinct types of horses have evolved quite naturally as breeders selected those which excelled in the various types of performances, and so it has come about that in horses perhaps more than in any other class of livestock "type is production." Draft power calls for a compact, heavy, low-set, heavily and short-muscled and -boned animal with a relatively docile and quiet type of nervous organization. Speed calls for a lithe, lean, relatively long-muscled and light-boned animal with a quick, nervous disposition. Grace calls for a well-balanced and rounded symmetry, stylish leg and foot action, and an inbetween type of nervous organization. The individuality of the animal, its phenotype, because this so closely correlates with its performance, is and should be the most important consideration in selection.

Pedigrees, if relatively complete in terms of records of performance (work, speed, show winnings, etc.), can be of very great usefulness in providing a safer basis for selection; and progeny performance, as in all classes of livestock, provides the one unassailable test of an animal's breeding merit. Performance records are available for various types of racing horses, which provides something comparable to milk production records in cattle. To a limited extent, show winnings are available for heavy and light harness horses and saddle horses. The dynamometer is available for the testing of draft power in heavy horses, but thus far

it has not been used in any practical way to help in the selection of draft horses.

The principles of inheritance in horses are similar to those in all other classes of livestock. The horse is the product of its genes times its environment. In this class of livestock, the environment in the form of training plays a much more important part than is true in any other class of livestock. Proper feeding is essential if any animal of any class is to grow out to the normal set by its particular genes. Cattle, sheep, and swine require no particular training, whereas training in the horse is fully as important as good genes. An offspring of Dan Patch and Lou Dillon would hardly be expected to do 1 mile in 2 minutes if it had grown up on pasture and spent the years from three to five pulling a grocery or laundry wagon.

More also in horses than in other classes of livestock do we need balance between the several parts of the body and between the physical and the mental make-up. We can overdo compactness in a draft horse until we reach the point where we have an animal that cannot move effectively. We want length of leg in a race horse, but we can reach the point where further increase in length of leg detracts from rather than adds to speed. Likewise, we can have too phlegmatic a draft horse or too high-strung and nervous a Thoroughbred.

The halving and sampling nature of inheritance prevails in the horse as well as complex interactions between groups of genes providing favorable and unfavorable nicks. We still have far too many horses ill-adapted, both from a genetic and from a training standpoint, for the purpose they are supposed to fill. With the number of horses declining, temporarily at least, it is of great importance that we use all means available, and perhaps design new ones, to measure both the performance and the transmitting qualities of those remaining, so that the less efficient may be the first to go and the better genes discovered and put together in more desirable and homozygous combinations.

Buying Horses.—Buying a horse even for the initiated is something of a gamble, whereas for the novice it is an extreme hazard. This is due to the fact that, in the short space of minutes or hours with the knowledge that many faults can be temporarily covered up through clever manipulation, we must evaluate a complex physical and mental make-up for use over long hours of work through days stretching into years.

As with all other classes of livestock, the first consideration is that of general health. Horses that have been shipped or have passed through sales stables may have had the opportunity of picking up various germs such as those causing pleuropneumonia (shipping fever) or influenza. Such ailments very seldom prove fatal, but, if carried home to a group of horses, considerable inconvenience may be caused.

Since the horse is maintained for his ability to transform energy into useful work or to provide pleasure and companionability, one of the most important things to be appraised is his disposition. Whether or not there are genes for obnoxious dispositions in animals or man is not known, but something does occasionally give rise to bad dispositions, and whether genetically or, probably more often, environmentally caused we do not want them. Undesirable dispositions may manifest themselves in the stall as halter pulling, kicking, biting, crowding, stall walking or trotting, weaving, cribbing, wind sucking, manger chewing, tail rubbing, etc. and outside the stall as an unwillingness to be harnessed, balking, running away, stumbling, etc. Work becomes doubly hard when it must be performed with the aid of recalcitrant beasts, and in a horse maintained for purposes of pleasure the first prerequisite is good manners. Even if not dangerous or particularly obnoxious, many of these faults and vices consume considerable energy for which the owner gets no return.

In addition to securing healthy horses that are free from objectionable manners and vices, one must, of course, select horses whose types fit them for the specific functions that they are intended to fulfill. This, of course, has many gradations from ponies to draft horses. Limitations of space and the general availability of excellent discussions on types of horses for specific requirements in book and bulletin form make both impossible and unnecessary similar discussions at this point. Since the value of a horse depends so largely on his ability to move from place to place, his feet and legs should receive first and major attention or, said more concisely, "no foot, no horse." Fully as important, however, are the matters of sound wind and good eyes. Any unsoundnesses of feet or legs, inability to breath easily and normally, or any impairment of vision should be avoided in purchasing horses. Since he is not a gift horse, better look in his mouth too in order to check on the soundness of his teeth as well as his age.

One final consideration remains, after having checked on a horse's freedom from vices, his disposition, his soundness of foot and limb, wind, mouth, and eyesight, his action, his general type of build as to the work or service it is intended to have him perform, *viz.*, his adaptability for specific work.

A horse may possess proper conformation, be sound, and have good action yet still not be well adapted for a specific work; consequently it is very essential that he be thoroughly examined at the work for which he is wanted. If the horse is to be used for heavy hauling for draft purposes, steady pulling under all conditions is an indispensable quality. For harness use the horse should drive promptly and freely with an easy, rapid gait and an alert expression, taking just sufficient hold of the bit to be in hand without causing the driver to pull on the

lines. The saddle horse should have an easy, prompt mouth, style, graceful carriage and should stand quietly to be mounted and dismounted.

Some horses are difficult to harness and object to taking the bit in their mouths; others jump when an attempt is made to place a saddle or harness on their backs; while still others offer a great deal of resistance to having the crupper placed under their tails, which, if due entirely to general muscular strength and tension, may be an indication of endurance. While being hitched up or mounted the horse should stand quietly and should start promptly but quietly on command. For any purpose the following vices should cause the animal to be rejected: balking, backing, rearing, kicking, striking with the forefeet, or running away. Less important vices are: throwing the head up or down, shying, scaring, breaking loose when tied, resting one foot upon the other, grasping the bit between the teeth, rolling with the harness on, or switching the tail over the lines. Occasionally the last named vice causes the horse to kick, in which case it becomes dangerous.

Enlargements or scars (due to deformity, unusual mishap, or uncommon disease) not conforming to any of those discussed should cause a horse to be rejected unless the nature of the cause and the detriment to the value and usefulness of the animal is self-evident.

Experience gained by examining large numbers of horses will aid in quickening the eye and judgment, thereby making it possible to perceive readily any unusual condition, but it should be remembered that a hurried examination is liable to prove a disappointment: consequently plenty of time should be taken in making the examination, because time is much cheaper than money tied up in an unsatisfactory horse. In some countries nine days are allowed by law to the purchaser in which to learn of the serious forms of unsoundness or vice in a horse, so that in this country it would seem fair to allow at least a day for a trial when practicable.

If possible, get a history of the animal, and while you are about it get a history of the person having it for sale. So many defects may be covered up by such unfair methods as drugging that it is a good plan to make purchases only from persons with good reputations.

Horses offered at auction sales should preferably be thoroughly examined previous to their being brought into the ring; at least they should be tried out in compliance with the rules of the sale before time for settlement.

Finally, it is well not to form the habit of seeing only the defects, for horses, like people, are seldom perfect; consequently in judging them weigh the good qualities against the bad. A horse should be valued by the amount of service it will perform rather than by its minor shortcomings.[1]

In case of the purchase of mares intended to serve in whole or in part as brood mares, attention should be given to their pedigrees, their collateral relatives, and their offspring in addition to their own individuality.

Breeder Must Know His Own Band First.—In spite of the fact that horses by and large have been selected on the basis of a phenotype

[1] Reese, H. H., How to Select a Sound Horse, *U.S. Dept. Agr. Farmers' Bul.* 779, pp. 21, 22.

lending itself to the efficient performance of specific tasks for a considerable period of time, they are as yet far from homozygous for desirable genes. The best appearing mare may not beget the best type foal when bred to stallion A although she might if bred to stallion B. As mentioned in Chap. XXII, it is a worth-while and sometimes very surprising exercise to lead out our animals by families, standing the foundation female at the head of each separate female line and arranging her offspring behind her so that all the offspring of each successive sire used will form a line at right angles to the female lines. This is easily done with horses and provides the opportunity for studying the whole band of mares with their offspring, of sizing up and evaluating the contributions

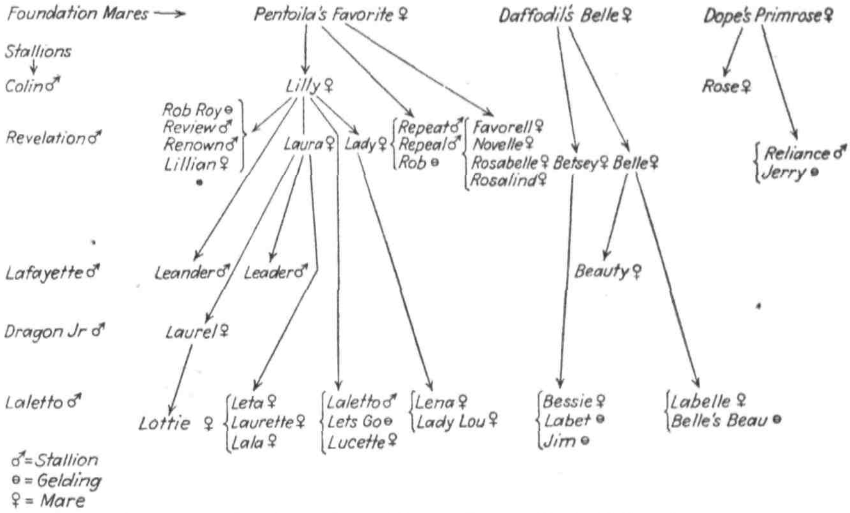

FIG. 182.—Breeding chart of Massachusetts State College horses.

of both sires and dams and arriving at an estimate of the good and bad features of the group as a whole, and of visualizing the trend which the group as a whole is apparently taking.

The story of the Percheron breeding at the Massachusetts State College is shown diagrammatically in Fig. 182. Two closely related mares, Pentoila's Favorite 164611 and Dope's Primrose 163421, born in the spring of 1920, were purchased from Ohio State University in 1923. The dam of the latter was the maternal granddam of the former, while the maternal great grandsire of both was the same animal Diamant 30018, and both mares were sired by Libretto 121447. They therefore were 40 per cent related. Both mares were in foal to Colin 166024, a grandson of Carnot 66666, when purchased and dropped filly foals, Lilly and Rose. These two mares (see Fig. 182) together with their

filly foals appeared to be an excellent foundation for a band of Percherons together with a good homebred mare Daffodil's Belle.

However, the Dope's Primrose line quickly faded out. She was fifth Futurity filly at the International in 1921, fifth three-year-old mare at Ohio State in 1923, second aged mare at Eastern States Exposition in 1926. Besides her daughter Rose by Colin born in 1924, she left two colts by Revelation 181000, called Bay State Reliance 204527, which was first as a colt in 1930 and as a two-year-old stallion in 1932

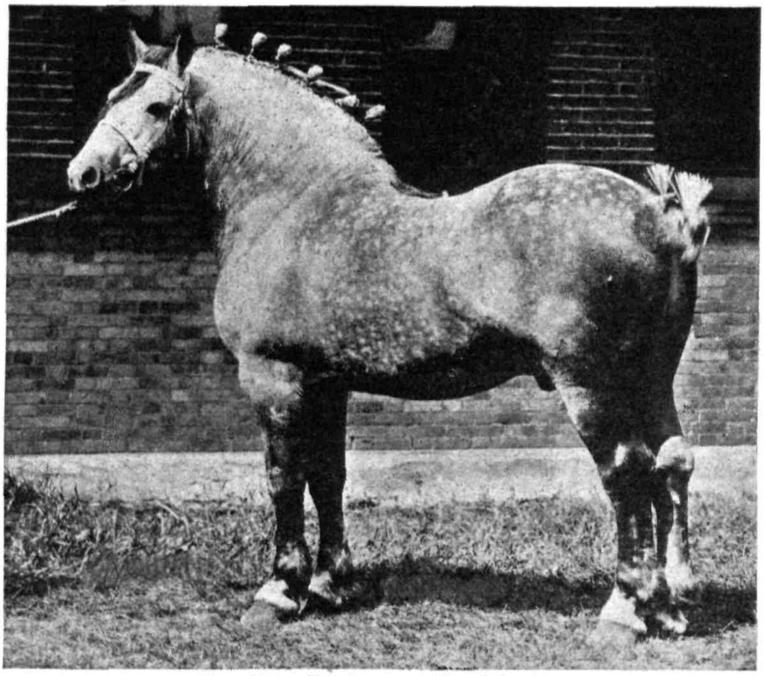

FIG. 183.—Percheron stallion Libretto.

at Eastern States and sold as a stallion, and Jerry, a male born in 1927 and used on the farm as a gelding. She did not conceive to breedings in 1924, 1925, 1928, and 1930 and bore a dead male foal in 1928. Her daughter, Bay State Rose, 186214 bore a male colt in 1928 that was altered. She failed to breed in 1928 and thereafter was used as a work horse until 1938 when she was sold. Dope's Primrose was sold in 1932. This mare although a good individual and purchased as a foundation mare made no contribution to the herd, and her line has entirely disappeared.

The other mare, Pentoila's Favorite, has been a fairly successful brood mare through having left one really good daughter, Bay State Lilly,

186213 by Colin in 1924. Pentoila's Favorite left 2 other daughters, Favorell and Novelle, by outside studs, which were not kept because of deficiencies in type, as well as 2 by Revelation 181000, *viz.*, Rosalind in 1928 and Rosabelle in 1929. Rosabelle dropped 1 filly foal that was sold, and she herself was sold in 1934. Rosalind dropped 3 dead foals, also 2 that went bad behind and 1 filly that was sold. In addition to these 5 females, Pentiola's Favorite also dropped 5 stud foals, 1 of which died as a foal, 1 was altered, and 3 were sold as stallions. Pentoila's Favorite was first-prize filly foal at the Ohio and Indiana State Fairs

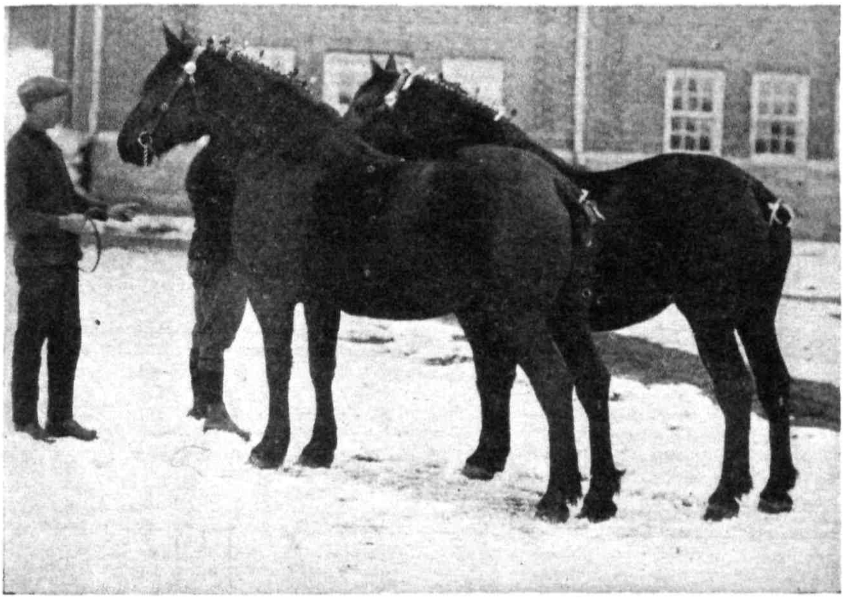

FIG. 184.—Foundation mares, Dope's Primrose and Pentoila's Favorite.

in 1920, third filly at the Percheron International Futurity in 1921, junior and reserve champion at Indiana in 1921, first-prize aged mare at Eastern States in 1924.

Bay State Lilly 186213, a daughter of Pentoila's Favorite born in 1924, has been the most outstanding brood mare at Massachusetts State College for the past 15 years. She was first-prize aged mare in 1931 at Eastern States, first and grand champion in 1932, second-prize mare in 1933 and 1934, and first-prize mare and foal from 1928 to 1933, inclusive. Four of her sons have been sold as stallions (Review, Renown, Leander, and B. S. Laletto); 2 are working geldings on the farm (Rob Roy and Let's Go). One daughter, Lillian, which had been first as a filly and yearling at Eastern States and second as a two-year-old, was sold.

Two other daughters of Lilly, Laura and Lady, by Revelation 181000 have been used as brood mares at Massachusetts State College. Laura was third-prize filly foal at Eastern States Exposition in 1931, first-prize yearling in 1932, and stood second in 1933, first in 1934, second in 1935, fourth in 1936, second in 1937, and first mare and foal in 1940. One son, Leader, by Lafayette 204281 and one daughter Lala by Laletto 208524 have been sold as breeding animals, and one daughter Laurel by Dragon Jr. 113939 and 2 by Laletto 2085424, Leta and Laurette, are now young

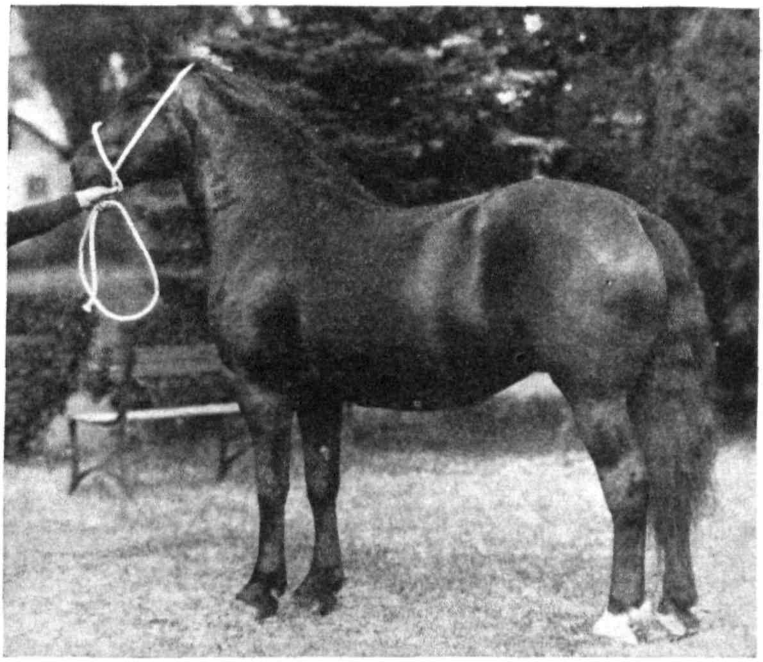

FIG. 185.—Percheron mare Bay State Lilly.

brood mares on the farm. Their type through their rear quarter and the set of their hind legs, however, makes it probable that they will not be kept as brood mares.

The other retained daughter of Lilly was called Lady. She was first filly foal and junior champion at Eastern States Exposition in 1932, first in her class in 1933, second in 1934 and 1935. Her first colt in 1935 by Dragon Jr. was altered, her second and third colts by Laletto in 1936 and 1937, Lena and Lady, are young brood mares on the farm, the latter having been first-prize two-year-old mare and junior champion at Eastern States Exposition in 1940. Lady was sold in 1938 because of a bad front foot.

The third foundation mare, the homebred Daffodil's Belle, has been an average good brood mare. Her daughter Betsey by Revelation 181000 was second-prize foal at Eastern States in 1931, but she and all her off-

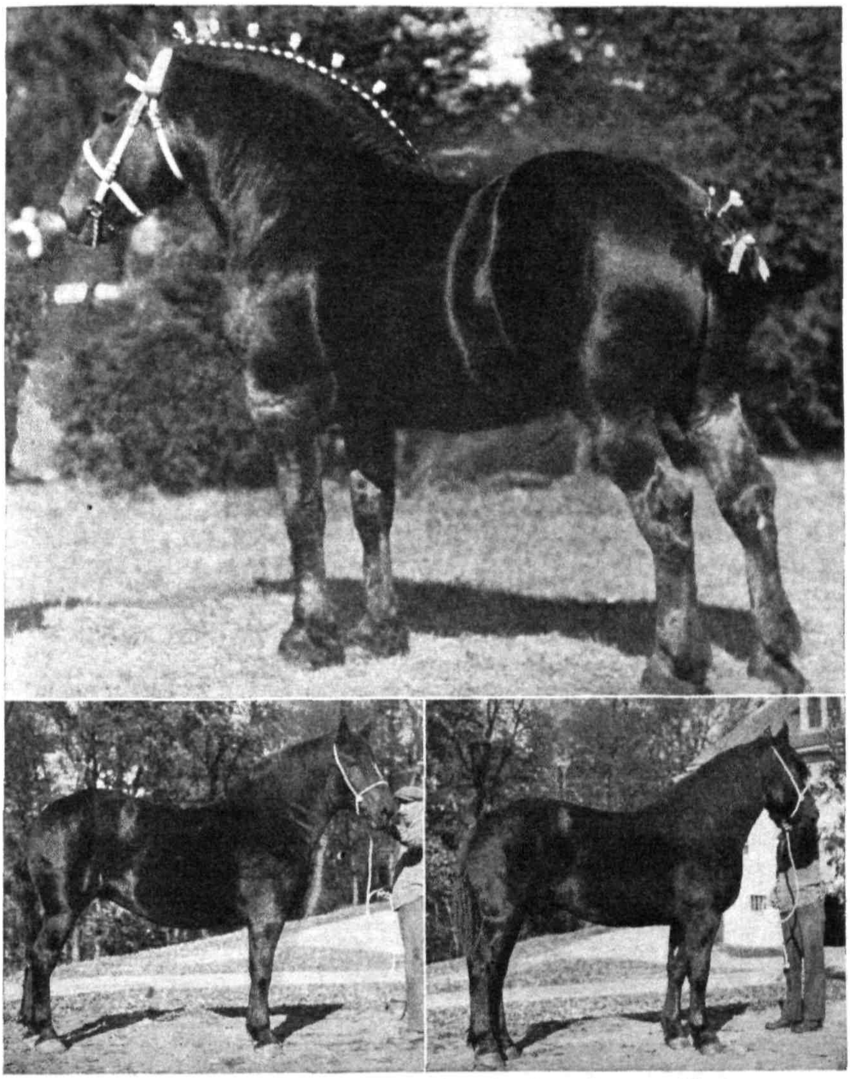

FIG. 186.—Revelation and his two best daughters, Laura and Lady.

spring have been sold. The other daughter, Belle, also by Revelation 181000, was not shown. She and her daughter Labelle and her gelding son Belle's Beau are still in the herd, but all will probably be culled and no offspring saved.

So, after a start with three foundation mares in 1923 and the purchase and use of three stallions (Dragon Jr. having been borrowed for a short time), we now have a seventeen-year-old mare Lilly, the best individual mare we have had and a fairly good transmitting mare, her ten-year-old daughter Laura, an excellent individual but not a good transmitter, making it probable that her 3 daughters Laurel, Leta, and Laurette will be culled, and another three-year old daughter, Lucette, as yet untried as a breeding mare. In addition we have 2 daughters of Lady (full sister to Laura) which are of excellent type but again untried as breeding mares.

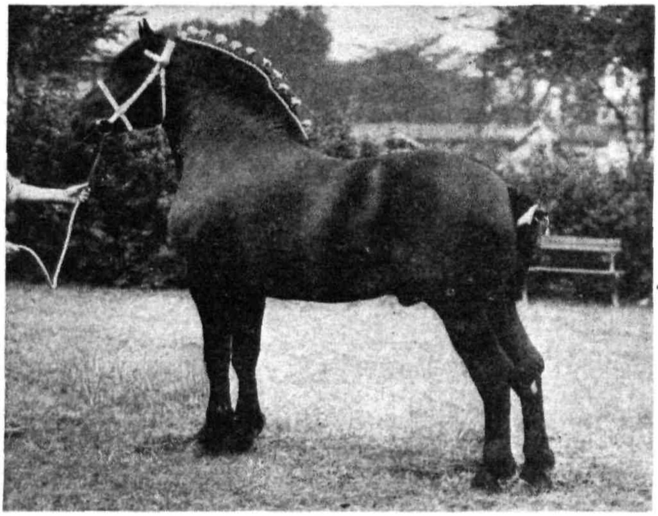

FIG. 187.—Lafayette, the grand champion Percheron stallion, Eastern States Exposition, 1933. Owned by Massachusetts State College.

We have bred and raised a lot of horses since 1923. Most of these animals have been used on the farm and have done their work in an acceptable manner. The stallions have been carefully selected in regard to their individual type and have cost from $1,000 to $1,500. Revelation 181000 was used for 7 years (1925 to 1932) and sired 2 very good offspring, Laura and Lady, a lot of good ones, and some poor ones. He was an imported horse that stood second to Hesitation, the grand champion at the International in 1923. He was grand champion at the Eastern States Exposition in 1925, 1926, 1927, and 1930.

Lafayette 204281, a son of Sir William 168112, he by Laet, was used from 1932 until his death from coronary thrombosis in 1935. He was grand champion at the Eastern States Exposition in 1933 and 1934. He was an excellent individual but left no impression in our herd, leaving only 1 daughter which was culled.

Laletto 298524 was purchased in 1935 and is still standing at Massachusetts State College. Like Lafayette 204281, he is a grandson of Laet 133886, and his dam is by Libretto, the sire of the two originally purchased mares. There is, therefore, just a slight trace of line breeding to Libretto 121447 in the pedigrees of the daughters of Laletto at present in the herd. Laletto was third-prize aged stallion at Eastern States in 1936 and 1937 and senior champion in 1941.

As is indicated in the above discussion some of the female lines are better than others. A glance at Fig. 182 shows that practically all the

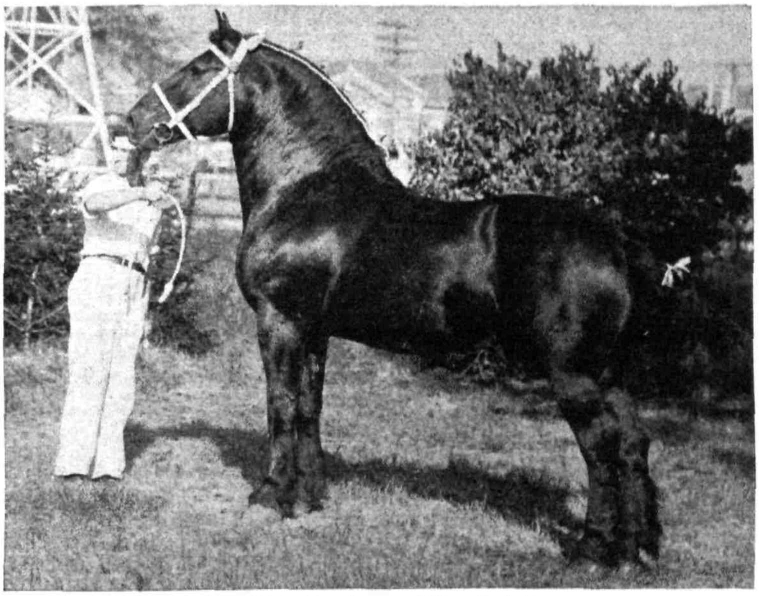

FIG. 188.—Percheron stallion Laletto.

animals represented, except a thin line starting at the bottom with Lena, Lady Lou, and Lucette and going on up through Lady and/or Lilly to one of the original mares Pentoila's Favorite, have been or will be sold or culled out because of various type deficiencies. As previously stated these culled animals have been good work horses, but they have lacked one or many things that would make them wholly acceptable from a draft type standpoint. The story has been told here for the purpose of illustrating the fact that rapid progress in the breeding of a species of animals that reproduce at such a slow rate as does the horse is hardly to be expected.

Selecting the Fillies to Save.—Only after a breeder has made a close study of the mares in his own band with suitable records and tabulations of their strong and weak points is he in a position to start on his search

for a stallion to mate with them. It is obvious, of course, that the male should be selected both on the basis of holding the desirable qualities which the breeder already has and also, and more especially, of bolstering the weak points shown by the mares. The mares at Massachusetts State College have from the beginning been a little too light in bone and a little too shallow to suit us. In addition there is a tendency for the hind legs to be a little close together and not to set under the horse as much as they should. In our search for our next stallion, these points will receive major attention.

In selecting mares or fillies either from outside or in one's own herd, acceptable type for the class of horse concerned should of course be the first criterion regardless of the fact that mares do not always breed exactly as they look. In other words, one has a greater expectancy of getting drafty offspring from draft mares than from thoroughbreds, and vice versa.

In addition to acceptable type, one should try to select from good female lines in which as many as possible of the animals have been of the desired type. An obvious weak point in the Massachusetts State College horses, as discussed above, is the fact that Pentoila's Favorite had 4 mediocre daughters and 1 good one, Lilly. Lilly in turn had 2 mediocre daughters and 2 good ones, Laura and Lady, and the latter, a somewhat poorer individual, is evidently transmitting in a more acceptable fashion than her somewhat superior typed sister Laura. In this whole female line, there are evidently both good and bad genes, the former not being as numerous as one might wish. It is very important therefore that both the direct ancestors (those occurring in the pedigree) and the collateral relatives (half brothers and sisters, cousins, aunts, uncles, etc.) receive some consideration. Because, generally, only the most acceptable animals are saved and used for breeding purposes, the pedigree of the direct ancestors of an animal is bound to look pretty good and will tell us in general the best that we can expect. The collateral relatives, on the other hand, which do not generally appear in the pedigree or if included contain only the desirable references, will tell us some of the bad things we may expect by selecting in their family. The pedigree of the Massachusetts State College filly Leta can be made to look very good as is shown in Fig. 189.

The pedigree (page 625), with some of the better show winnings listed, looks very good. How about some of the collateral relatives? Pentoila's Favorite had 1 good daughter Lilly and 4 not very good ones; 1 good son, 2 or 3 average ones, and 1 poor one. Lilly had 2 good daughters and 2 mediocre ones, 6 sons ranging from good to poor. Revelation had quite a range of offspring, making his total breeding value about average. Laura's offspring on the whole (4 daughters and 1 son) have

not been nearly so good as their dam in draft quality. Laletto has sired a range of offspring from very good to very poor. Leta, the filly pedigreed in Fig. 189, is a fairly good individual, but she is not so good as Fig. 189 makes her appear, and, although she has some good genes, it would seem from a study of her collateral relatives that she probably also has a lot of poor ones and would probably not be a particularly successful breeding or transmitting mare. Complete pedigrees in terms of record of performance of both direct and collateral relatives can be an important aid to selection based first of all on individuality.

- Leta, 1st prize foal 1937
  - Laletto, 2d prize Ohio, Indiana 1935, 3d prize Eastern States Exposition 1936, 1937
  - Laura, 1st Eastern States 1932, 2d Eastern States 1933, 1st Eastern States 1934, 1st Eastern States 1940
    - Revelation, 2d International 1932, Grand champion Eastern States Exposition 1925, 1926, 1927, 1930
    - Lilly, 1st prize Eastern States 1931, 1st and grand champion Eastern States 1932, 1st mare and foal 1928–1933, inclusive
      - Colin
      - Pentoila's Favorite, 1st filly Ohio and Indiana 1920, Junior and reserve champion Indiana 1921, 1st mare. Eastern States Exposition 1924

FIG. 189.—Good-looking pedigree of Leta.

The real test of a breeding animal is, of course, its ability to transmit its own desirable qualities. This is the progeny test, which should be utilized wherever possible to do so. If we can find good individuals, whose complete pedigrees will bear the light of careful scrutiny and who have demonstrated their ability to transmit their own good qualities, we are on perfectly sound ground in making our selections, although we have yet to learn how this triply desirable animal will nick with one of our own. Obviously, it is not always possible to get all this information, in which case a breeder should get all the information available and then "cross his fingers" until he sees how things pan out.

In the selection of brood mares, it is essential that attention be given to their probable and actual ability to bear young over a long period of years. Their probable ability in this regard can best be judged from their complete pedigrees (both direct and collateral relatives). In other words, in the selection of mares one should select only in families that have a high natural rate of fertility. Like all other attributes having a genetic basis, this varies among different families in all the classes of livestock. Demonstrated abilities by the direct and collateral relatives is the best guarantee that a breeder can get for any new animal going into his band of females.

Actual ability to reproduce can be ascertained from the performance of older mares as well as from current examinations of their genital tracts by competent veterinarians, and the latter type of examination can and should be used on young mares.

Finally in the selection of mares or fillies that hard-to-describe quality of femininity should receive considerable emphasis. The general term for it is probably *quality*, as evidenced in fineness of bone (different of course with different types of horses) and fineness of hide and hair together with indications of alertness and intelligence and a certain nobility of carriage and demeanor. The mare should be well-balanced throughout with a roomy middle and ample width through the hips and croup and must have a sound, well-developed udder.

Selecting the Stallion.—The safest plan in securing a stallion is obviously that of getting one that has already demonstrated his ability as a sire in the type and performance of his get, in other words, a proved sire. Unfortunately not many good, proved stallions are available at any price. Most breeders, therefore, will have to select and use young unproved studs.

These should be healthy, of the desired type and disposition from a naturally fertile strain. Preferably they should be by a proved stallion, the majority of whose offspring were desirable and out of a daughter of a good proved stallion, said daughter having preferably demonstrated her ability to transmit desirable qualities to her offspring. Admittedly, such animals are scarce, complete records of ancestors not generally available, etc. Nevertheless we must make a start sometime in getting such information, and it is unlikely to become available until prospective buyers start asking for it.

Just as indications of femininity are desired in the female, so do we desire indications of masculinity in the stallion. Here we expect a little more compactness and scale, a little heavier bone, a well-developed forequarter and chest. We want spirit and masculinity in our stallions but of a sort that proper training has rendered obedient.

Sire Indexes in Horses.—As yet few objective measurements of performance that might serve as a basis for an index have been developed for the horse. H. H. Laughlin has evolved a mathematical yardstick for measuring racing capacity in the Thoroughbred through a study of the breeding and racing records of some 10,000 of these animals. He has measured quality of performance for a single race on a definite mathematical scale by developing correction factors for sex, age, weight carried, distance run, and speed, on the basis of actual performance of this breed under varying conditions and yielding standards that are the "smoothed best" which the breed has accomplished up to the present time. By means of such standards the true racing capacity of any horse can be measured, and, if he runs a sufficient number of races under standard conditions, the one figure for racing capacity (derived from the several "quality of performance" figures for separate races) can be compared with a similar figure for any other horse, and the question as to which was the better racing horse can be definitely answered, although the two horses may have never raced against each other.

When the racing capacities of a male and female together with their close, direct, and collateral relatives can be ascertained, then it is possible to formulate a futurity index or hereditary-promise level for their offspring. Because racing capacity involves the whole organism, it is reasoned that multiple genes are concerned, and therefore equal weight is given to both the sire and dam in arriving at the futurity index of their offspring. In this system the breeding factor of the sire is obtained by taking one-third of the average racing capacity figure of his sire and dam plus one-third of the racing capacity of the sire himself plus one-third of the average racing capacity of the foals that he has already sired. The breeding factor of the dam is arrived at by a similar procedure, and the average of the sire's and the dam's figures is called the *futurity index* of their potential or actual offspring. This "prediction-index, when it contains only a few ancestors, each doubtfully stressed, gives a low prediction-value; but when it comprises a highly representative group of close antecedent blood-kin, each properly stressed, then the prediction-value of the specific formula is high."[1]

It would, of course, be possible to work out similar prediction values for any type of racing horse, where the one criterion for selection is that of speed, or for show horses, where the criteria are type, action, and manners, provided accurate and complete records of performance are available.

Phillips, Brier, and Lambert have made some preliminary studies of tests designed to measure the speed and efficiency of light horses. The

[1] LAUGHLIN, H. H., Racing Capacity in the Thoroughbred Horse, *Sci. Monthly*, **28**: 210, 310, 1934.

tests were designed to measure speed, both at the walk and trot in carriage and at the trot under saddle, length of stride, and respiration and heart rate before and after exercise.

From the results it is evident that tests designed to measure speed, length of stride, and respiration and heart rate are subject to rather wide variations when applied to the same horse at different times. It is apparent, therefore, that, if such tests are used for the purpose of detecting differences between horses, the tests must be repeated several times under carefully controlled conditions. However, the degree of accuracy required will depend upon the magnitude of the differences that it is desired to detect. In most of the analyses presented here, the variability of the material used (*i.e.*, of the 14 horses) relative to the various sources of error was high enough that the observed differences between horses were significant. In a more uniform group of horses it would probably be necessary to improve the accuracy of the test in order to differentiate with any degree of certainty between animals with respect to any given character.

It should be emphasized that the results presented in this bulletin deal only with the degree to which results of each of the tests agree when obtained on the same horses at different times. Before these tests, or any other tests of performance, should be applied generally, careful studies are needed to determine the relationship of the tests to actual performance under practical working conditions.[1]

Although the machine has replaced the horse as a source of draft power to a very considerable extent, there is unmistakable evidence that interest in light horses for pleasure and sport is on the increase. No better safety valve for the effects of our high speed, machine civilization can be imagined. It is to be hoped that much of the former breeding of draft horses in our farms can be gradually replaced with the breeding of light horses. This is a new field which has opened up in the past few years and one that seems to hold much in the way of possibility especially for farmers located near the large centers of population.

In the draft horse, we also need objective tests for measuring working abilities. These animals exist for the one purpose of doing useful work. As stated by Phillips, Krantz, and Lambert,

Objective measures of the characteristics which contribute to maximum ability to do work are badly needed. Such measures might include maximum pulling ability for a short period of time, staying power with a heavy load over long periods, walking speed with a standard load over a given distance, and ability to maintain weight doing a given amount of work with a given allotment of feed, along with careful records of the occurrence of soreness and unsoundnesses. When such methods are developed and a sufficient number of records is obtained

[1] Phillips, R. W., Brier, G. W., and Lambert, W. V., A Study of Some Problems Involved in Measuring Performance in the Horse, *U.S. Dept. Agr. Bur. Anim. Ind.*, Mimeographed Rpt.

under standard, experimentally controlled conditions of training and testing, and the animals used have been scored and measured at comparable ages, it will be possible to arrive at some estimate of the value of any given measure or score.[1]

The dynamometer is available and has been used for many years to get the maximum pulling ability of horses for a short period. Records of these contests together with measurements of the animals competing have shown definite correlations between height and weight and ability to pull, but no other measurements have shown definite positive correlations. "Staying power with heavy loads over long periods" and "walking speed with a standard load over a given distance" might also be secured by means of the dynamometer.

So far as the writer knows, the dynamometer has not as yet been used in any constructive manner as an aid in the selective breeding of draft horses. The dynamometer contests[2] are a very interesting sporting event and generally draw a much larger crowd then does the orthodox judging of horses on the basis of type. In fact, it has happened more than once that the type judging has had to be temporarily suspended until the breeders and showmen of the purebreds have returned from watching the pulling contest. In other words people in general are more interested in seeing what a horse can do than they are in admiring him for what he may look like.

Type in Horses.—Horses have been selected on the basis of the type best suited to perform given tasks for hundreds of years. This has led gradually to the creation of distinct and separate types for racing, riding, driving, and pulling. Selecting the speediest horses gradually produced the racehorse type, selection for power gradually produced the draft-horse type. The speed and saddle types are now definitely established, and there seems to be little prospect that they will be changed in any fundamental way. The task of the future in these types, then, is further refinement to add slightly to their speed, symmetry, balance, action, and behavior; and by means of keener selective tools based on records of performance, measurements, and progeny tests to render them more homozygous for the respective qualities desired.

The draft horse was created by selection for the particular purpose of moving heavy loads at a fair speed. For this task the criterion was the greatest weight possible in the smallest compass. The heavy draft horse was a remarkably efficient animal for the job he was supposed to do. The railroads, trucks, and tractors have made their appearance

[1] Phillips, R. W., Krantz, E. B., and Lambert, W. V., The Accuracy of Measurements and Scores of Draft Horses, *Amer. Soc. of Anim. Prod. Proc.*, 1938, p. 82.

[2] See Phillips, R. W., Madsen, M. A., and Smith, H. H., Dynamometer Tests of Draft Horses, *Utah Agr. Expt. Sta. Cir.* 114, 1940.

during the past 100 years, however, to challenge the horse in this field, and largely because of their greater speed they have supplanted him so that the market for the ton-upward horse has shrunken almost to the vanishing point. Draft-horse type, in other words, is changing to a somewhat smaller, more active model. In particulars, the type will remain what it always has been, a short, compact, well-set-up, and straight-moving type, but, in place of weighing from a ton upward, he will weigh from a ton downward. He will be a medium-sized draft horse, for the city market for the heavy sort has disappeared, the farmer never did like the extremely big ones, and in so many instances now power machinery has to do the very heavy work. The new type will stand 16 to 17 hands, the stallion weighing 1,900 to 2,100 lb., the mares 1,700 to 1,900 lb. in good condition.

There are two ways of creating such a horse, one by mating large stallions to small mares (or small stallions to large mares) and the other by mating medium-sized stallions to medium-sized mares. If the former method is used, and we put in the two extremes, we will generally get the mean in the immediate offspring, but the mixed inheritance of these animals can be expected to come out in all sorts of combinations in their offspring. In other words, we can expect to have to do a lot of weeding out if such a plan for creating the medium type horse is used. Because the average run of farm mares tends to be on the small side, there would still seem to be a place for the big stallion.

The other plan of mating medium size to medium size should give less extreme variations and lead more quickly toward the desired goal.

With the system either of mating unlikes to produce a medium or of mating intermediates in types, it goes without saying that selection must be practiced and the offtype animals discarded. Less of this will be necessary with the matings of animals that resemble each other closely in general type. One should not deceive himself, however, by thinking that two animals which are similar in appearance are also similar in their genetic make-up. Many different combinations of genes may give the same general phenotypic appearance. We must remember that, in dealing with commercially important characters of our animals, we are probably dealing with hundreds or thousands of genes. This is very different from crossing a rough, white guinea pig (*RR bb*) and a smooth, black one (*rr BB*) and getting rough, black offspring (*Rr Bb*). And even in this simple case, dominance interferes with our progress, because we cannot distinguish offhand between the following rough, black guinea pigs (*RR BB*), (*RR Bb*), (*Rr Bb*), (*Rr BB*). We have no conception of the dominance, partial dominance, epistatic, and other probable interrelations involved in the thousands of genes in our larger animals. There are many combinations of coins that will make a dollar,

e.g., 10 pennies, 4 nickels, 2 dimes, and 2 quarters or 5 pennies, 3 nickels, 3 dimes and 1 half dollar, etc. Likewise many combinations of genes may give the same phenotype.

We might use a somewhat farfetched analogy letting coins stand for genes. We might have two animals as A and B below:

A	B
10 pennies	12 nickels
4 dimes	4 dimes
2 quarters	
16 coins = $1	16 coins = $1

and each of these combinations might result in a good animal, because the pennies, dimes, and quarters of one react favorably together, and the nickels and dimes of the other also react favorably together. But each animal passes on only one-half of its own hereditary material to each of its offspring, so that in the above the offspring gets from one:

5 pennies	*and from the other*	6 nickels
2 dimes		2 dimes
1 quarter		
8 coins or $0.50		8 coins or $0.50

The total is again $1 but the reaction between 5 pennies, 6 nickels, 4 dimes, and 1 quarter is not favorable, *i.e.*, the resulting animal is not a favorable nick. If we are to create animals that will breed true, we must devise means of making our animals homozygous so that they will be more nearly alike genotypically as well as phenotypically and each pass relatively the same set of favorably reacting genes to each offspring. The best tool for accomplishing this purpose is some degree of inbreeding. In addition we know that the environment both before and after birth has very far-reaching influences upon the final form and performance of any animal, so that two animals with identical inheritance in the form of genes may be very dissimilar in final form and performance, and two other animals with very dissimilar sets of genes may be very similar in final form and performance.

If animals are to breed true, they must be made homozygous in the bulk of their genes. Mating animals which are alike phenotypically will have little effect in making them homozygous in their genes, and likewise mating unlikes will have little effect in making them more heterozygous in their genes. In short, whatever system is adopted for attempting to create a true-breeding strain of intermediate-sized draft horse must involve both selection and some form of inbreeding in order

to render the animals relatively homozygous or in the breeder's language to "fix the type."

This whole business of changing the type (weight) of our draft horses means many a headache for the judge in the show ring. It is going to take real courage to turn down a good big horse in favor of a good medium-sized one. The big one will excel in weight and draft power, the smaller one to offset this should be expected to excel in action and movability. Care must be exercised too that the desire for somewhat less weight than formerly does not express itself in either a chunk, easy keeping to be sure, but generally lacking in movability, or in an upstanding, light-boned, and light-middled animal which is apt to be a hard keeper, lacking in power and stamina, although probably excelling in freedom of action or movability. It is in just such situations as this one involving a change in type that the art of the breeder has its best opportunity of expression. If the art is backed up by or based upon a sound knowledge of the genetic principles involved, it will eventually evidence its inherent soundness. Art alone, however, is not enough (or it works too slowly with too many mistakes); nor is a knowledge of principles in itself enough. For constructive breeding at a tempo to suit the modern age both art and science are essential.

Breeding Efficiency in Horses.—In order that the breeder may have a clear picture of the breeding efficiency of his stallions and band of mares, careful records should be kept of the occurrence of heat periods in the mares, number of services required to settle each mare, percentage of mares settled by each stallion, birth weight of foals, duration of gestation, etc.

A study[1] of the breeding performance of 43 mares at the United States Morgan Horse Farm, Middlebury, Vt., from 1928 to 1938 shows that

132 mares conceived, foaled, and raised their foals.
10 mares conceived, foaled, but foals died before weaning.
6 mares conceived but aborted.
73 mares failed to conceive.
221 total mares bred.

Summarizing, we see that 221 breedings produced 132 foals which lived—a breeding efficiency on the part of these mares of 59.7 per cent in terms of livable foals.

In tabular form these studies give the following results for individual mares.

[1] Lambert, W. V., Speelman, S. R., and Phillips, R. W., The Reproductive History of the Stud at the United States Morgan Horse Farm from 1928–1938, *Amer. Soc. Anim. Prod. Proc.*, pp. 358–365, 1939.

TABLE 52.—BREEDING PERFORMANCE OF MORGAN MARES

Livable foals	Number times bred	Breeding efficiency	Livable foals	Number times bred	Breeding efficiency	Livable foals	Number times bred	Breeding efficiency
0	1	0	2	2(5)	100	4	6(2)	67
0	2	0	2	3(2)	67	4	11	36
0	3	0	2	4(2)	50	5	7(2)	71
1	1	100	2	7	28	5	11	45
1	2(3)	50	2	8	25	6	7	86
1	3(3)	33	3	3	100	6	11	55
1	4(2)	25	3	4	75	7	7	100
			3	5	60	7	8	88
			3	8(2)	37	7	9	78
						8	10	80
						8	11	73
						10	11	91

The breeding performances of 5 stallions that bred 12 mares or more are shown in Table 53.

TABLE 53.—BREEDING PERFORMANCE OF MORGAN STALLIONS

Name	Number mares bred	Fertility percentage
Delmont	28	75
Abbott	20	75
Mansfield	82	69.5
Bennington	46	56.5
Monterey	12	50
Average of 5	..	65.2

These Morgan horses, it is seen (both sexes), are only about 60 to 65 per cent efficient in terms of reproduction. The breeding efficiency of horses in general has been at about this figure for many years. It is a serious problem that probably will require considerable study and work for its solution. Obviously such a low breeding efficiency is a serious handicap in breeding this class of livestock.

Summary.—We have seen in this chapter that in spite of drastic reductions in the numbers of horses in the United States of America during the past 20 years, due to the inroads of various forms of mechanized power, the horse is still very much with us as a source of power on the farm, is still essential in modern war, and is filling an ever larger place in pleasure and sport. In the past, selection of horses has been based almost wholly on individuality. Because inheritance in horses follows

the one basic pattern found in all animate forms of life, we have now come to realize that sound selection must consider records of performance of direct and collateral relatives and of the animal itself in addition to the consideration of individuality. We are badly in need of practicable measures of performance in the horse. Only when these have been devised and put to work in the securing of essential records and the records used intelligently together with continued full considerations of individuality, will our selection in this class of livestock be on a sound footing. When the above methods have revealed the inherently better strains of horses, we will face the further task of intelligent line- and close-breeding, so that we may create fairly true-breeding strains.

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[1] See also Appendix A.

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CHAPTER XXV

SELECTION IN MEAT ANIMALS

In the days of extensive immigration into the United States, just before and after the turn of the twentieth century, this country was known among the poorer classes of Europe as "the place where a poor man can have meat every day in the week." Americans have always been hearty meat eaters, although some foreign countries surpass us in meat consumption. The development of our meat industry here grew out of the fact that we had extensive pasture land and could grow more grains than we could consume or sell abroad as such. In addition, meat in the form of live animals provided its own transportation before the days of steam and motor transportation systems.

Both meat and wool were produced along the Atlantic seaboard in colonial days. As the Alleghenies were crossed and the trek of the covered wagon progressed on toward the Mississippi, then on toward the Pacific, meat animals filled an increasingly important function in converting feed into food, hides, and wool, and the eastern portion of the country turned naturally to the production of milk, eggs, fruits, vegetables, tobacco, and cotton. Today the Middle West, the corn belt, together with the range country farther west is the center of meat production, two-thirds of the total supply being produced west of the Mississippi and two-thirds of it consumed east of the Father of Waters. Whether or not this situation will persist is a matter for the future to decide.

Now that scientific agriculture has (1) produced a beef animal which can stand excessive heat by the infusion of Brahman and Afrikander blood into the beef breeds, (2) has conquered the tick, and (3) has introduced crops such as Lespedeza and Kudzu which thrive on the poor, dry soils of the South, that region can be expected to develop a more intensive animal husbandry wherever internal parasites can be controlled. It is also being urged that our specialized dairy regions along the East and West Coasts diversify by means of a more inclusive type of animal husbandry. These movements, the recognition of the true value of meat in the human diet as the best source of protein and of many minerals, and its recently recognized role as one of the best of the so-called "protective" (high vitamin content) foods, together with its palatability for the great mass of people the world over seem to indicate that meat

will more than hold its own in the diet of the human, and that a great mass of humanity, heretofore limited in their ability to secure meat, will greatly increase the demand for meat when they succeed in securing the necessary purchasing power.

According to the 1940 census, there is a total of about 150 million meat animals to a total of 40 million horses, mules, and dairy cattle in the United States of America at present. In total bulk, they are of great importance both as converters of feed and conservers of soil fertility. In many instances, soil conservation implies the substitution of grass for clean, cultivated crops, and grass in turn implies livestock to consume it.

General Bases of Selection in Meat Animals.—Our discussion of the general principles of selection and some particular phases as they apply to dairy cattle and horses in the three preceding chapters has already entailed some repetition. Because the principles of reproductive physiology and inheritance are similar in the efficient production of meat animals and in the production of milk, power, speed, or beauty of form or action, it seems unnecessary to repeat again lengthy discussions of these matters in regard to meat animals. We will, therefore, merely remind the student in a brief manner that in practicing selection in meat animals, as in all others, attention must be given to:

1. The prospective market.
2. The breed or breeds seemingly best adapted to local conditions and market.
3. The matter of general health, longevity, and vigor.
4. The matter of genital health and regularity of breeding.
5. The prospect of natural fertility.
6. The type best suited for the sort of production intended.
7. The matter of uniformity of type, and "blood" if possible, in the foundation females.
8. The value of recorded meritorious performance in both the direct ancestors and the collateral relatives of the animals selected.
9. The necessity for proving breeding merit through progeny studies.
10. The necessity for properly evaluating environmental and hereditary influences.

Anatomically, meat type calls for a low-set, blocky, or compact sort of animal with the upper portion of the body and the rear quarters showing maximum development. This generally means a thick, well-developed forequarter as well, although this region of the carcass, in spite of the fact that it is fully as nutritious as the rear portions, generally sells for less over the counter. At least, this portion of the animal should not show overdevelopment, and there should only be the necessary minimum of head, neck, paunch, and leg. In the finished animal,

smoothness and evenness of contour, mellowness and fineness of fleshing, a proper degree of fat covering, and indications of quality in hair, skin, and bone are the qualities sought.

Physiologically, meat type calls for the animals' ability to consume a considerable quantity of feed above that required for maintenance, plus the added ability to turn this excess feed initially into rapid growth, later into a moderate outside covering of fat, and finally into a deposition of fat in the connective tissues in and between the various muscles of the body with as little fat as necessary deposited around the internal organs. And since the object in fattening animals is generally that of financial profit, we greatly desire that our animals be efficient feed converters and make the maximum possible return in carcass development for each pound of digestible nutrient fed to them.

That all classes of our meat animals show variations in type, rate of growth, efficiency of feed conversion, and quality of the finished product needs no elaborate discussion. Selection in these classes of livestock is based upon discovering favorable variations in these regards in order that the genes causing these favorable variations may be increased in number at the expense of the less desirable ones.

Meat animals possess one considerable advantage over dairy cattle from the standpoint of selection, in that in the former both sexes make evident, in their appearance, at least some of the things being selected for, *viz.*, the size of and relative proportions between the various parts of the body. To balance this, however, is the disadvantage that final judgment on quality of carcass, proportion and distribution of fat and lean cannot be ascertained until after the animal has been slaughtered, whereas the dairy cow yields a measurable product daily.

The easy recognition of general type has brought it about that individuality has been used almost exclusively as a means of selection in these classes of animals. Lately, however, recognition of the fact that animals do not necessarily transmit in full accord with their appearance, that phenotypes and genotypes do not necessarily coincide, plus the discovery of the halving and sampling nature of inheritance have begun to bring home to fat-stock breeders the necessity of bulwarking their individuality selection with records of performance of direct ancestors and collateral relatives and of instituting progeny-performance tests. Sound selection here as elsewhere must be based upon genes that cannot be studied directly but only as they manifest themselves in animals. How these animals transmit depends upon what their genetic make-up is, so that our task in breeding better meat animals, as in all others, is that of devising practicable means for determining genetic constitutions.

Meat animals that place high in the show ring do not always and necessarily sire good type animals. One of the best examples in this regard is the Shorthorn bull Avondale, which stood fourth in his class at the International Livestock Show yet had a much more potent influence on his breed through his descendants than any of the three bulls placed over him. Knapp has progeny-tested three rather closely related beef bulls at the Agricultural Research Center at Beltsville, Md. "One is a half brother to a Grand Champion, the second a son of the first, and the third was the son of the same Grand Champion, or, in other words, father, son, and nephew. On show ring standard they would have been placed in that order. On performance score, the half brother to the Grand Champion was by far the best of the three bulls and the other two reversed their placing on foot." We have recently had the same sort of experience with one of our breeds of sheep at the Massachusetts State College when the best type ram ever owned by the institution proved to be practically a complete failure as far as the all-important item of transmitting his own good qualities to his immediate offspring is concerned.

Individuality will continue to play a major role in the selection of meat animals, for it would be illogical in general to expect narrow, upstanding, hard-keeping animals to beget wide, low-set, rapidly fattening offspring. But animals of acceptable meat type can only transmit these qualities unfailingly to all their offspring when they have themselves been rendered relatively homozygous for the necessary genes through the use of the practical breeder's tools of selection and systems of breeding, a process which probably could be accomplished in the course of a long time through selection based upon individuality, but which fortunately can be greatly speeded up through the securing and intelligent use of records of performance. Individual selection, by itself, is rather a weak force in establishing any character, especially those so subject to nutritional and other environmental factors and, in addition, probably controlled by the interactions of a great many genes, as is no doubt true of most of the commercially valuable qualities of our meat animals. Individual selection is weak because it does not get down to the root of the matter, the genes, but deals rather in appearances and these may be very misleading. Even being misled only once in the choice of a sire may wreck the breeding efforts and progress of the better part of a lifetime unless the mistake is recognized early, which is not likely to be the case without the diligent use of a yardstick based upon records, and unless the breeder has the courage and is so situated financially that he can right his wrong by immediately eliminating the poor sire and all his offspring from the herd.

The producer of meat animals, perhaps more than breeders of other classes of livestock, needs an ideal toward which to strive just as did the instigator of the movement that led to the development of modern purebreds, Robert Bakewell, who was a keen student of form and function, was given to taking measurements and keeping records on his animals, and is said to have kept cuts from his animals in pickle in order to study transmitting abilities. There are ideals and ideals in animal breeding. The ideal set by the market changes with changing dietary habits, modes of living, and economic ups and downs. The breed associations attempt to formulate ideals for their breeders to follow, and these are stressed particularly in the show ring and at "type" schools. The packer has his ideal, which he tries to "sell" to the breeder. Ideals vary somewhat between regions and between groups of breeders. The commercial producer of meat generally has as his ideal the kind of animal that will make him the most money whether or not it coincides with any or all of the above. In addition to the possibility of there being many ideals, there is the added fact that the one or the many can and do change.

To all and sundry, consumer, breed association, packer, breeder, and farmer, it would seem sound to suggest that the ideal be made to rest basically on the efficient production of a high-quality carcass with as few whims and nonessentials as possible. It is difficult enough to be successful in breeding for utility without complicating matters through the inclusion of a lot of nonessentials and fancy points. Each additional item to be selected for reduces the chances of complete success manyfold.

In addition to practical ideals, the breeders of meat animals need practical yardsticks to measure individual and transmitting merit. Until these have been developed and put into use in securing factual data which can serve to prove transmitting abilities and can also be included in pedigrees, selection in meat animals will continue to be beset with many pitfalls.

Attempts to formulate practical "record of performance" procedures have been made during the past 10 years and are going forward at an accelerating rate at present. The ultimate goal is improved strains of livestock that will reproduce themselves with a high degree of uniformity. Various systems of breeding are being used experimentally, including closebreeding, linebreeding, and crossbreeding. The progeny-performance test based upon actual performance is the best and only sure method known of locating individuals that are prepotent for the qualities sought. If they cannot all be found in one individual, the separate items can be fused by proper systems of breeding, testing, and selecting.

In brief, what we seek in meat animals is a large quantity of high-quality product efficiently produced; or in specific terms, we want

animals of the correct type (proportion between parts) endowed with the internal mechanism that entails both a low maintenance requirement and an efficient conversion of feed in excess of maintenance into an acceptable product plus the ability to transmit these qualities regularly to their offspring, although even after our animals have been rendered relatively homozygous, we can still expect considerable variation. Our judging and show rings concern themselves only with type (proportion of parts and general symmetry) plus a modicum of attention to inheritance through "get of sire" and "produce of dam" classes. Most of our shows could and should be strengthened in the latter respect. In

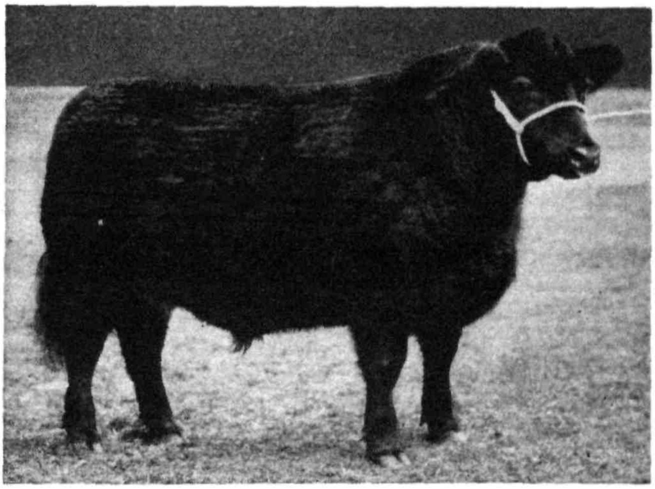

FIG. 190.—Briarcliff Model, the grand champion steer at the 1933 International Livestock Exposition and the second international grand champion bred, fed, and shown by Mr. Oakleigh Thornes, Briarcliff Farms, Pine Plains, N. Y. (*Courtesy of William H. Pew, Manager, Briarcliff.*)

dairy cattle, there is a slight tendency to include production along with type in judging. In meat animals there is undoubtedly more justifications for type judging than exists in the dairy breeds, but it would be very useful if some method could be devised whereby consideration could be given to production (efficiency of feed conversion) in meat animals as well as to their type.

Selection Indexes in Beef Cattle.—The fact that the market for many years has discriminated in price between prime, choice, good, medium, and plain animals, plus everyday experience, proves that there are wide differences in conformation and value between beef animals. Part of these differences are environmental, *i.e.*, due to differences in amount and kind of feed. Part of them also, as is well known, are due to inheritance. The dairy cow has been fashioned by

digestible nutrients per 100 pounds gain from birth to 900 pounds live weight, A—379.5, B—404, C—381 pounds; pounds of cold dressed carcass per 100 pounds total digestible nutrients, A—17.5, B—15.9, C—17.5; carcass grade, A—77.1, B—83.0, C—80.4.

In other words, the calves of sire A, when averaged, were best in weight for age, gain for feed consumed, and dressing percentage for feed consumed, but poorest in carcass grade.

The calves of sire B were poorest in weight for age, gain for feed consumed, and dressing percentage for feed consumed, but best in carcass grade.

The calves of sire C were second in weight for age, gain for feed consumed, and carcass grade, and equal to A in dressing percentage for feed consumed.

These data are from four, two, and seven calves respectively, from each sire, and of course they can be considered only as indications of sire differences. This is especially true when one considers that the dams were different in most cases in each group, a point of very great importance . . .

These investigations bring to light many experimental difficulties which are important in connection with the development of more practical procedures for record of performance with beef cattle. One of the chief difficulties is that nearly all of the tests are made on steer calves, and hence the most efficient feeders and those having the highest carcass grades cannot be used for breeding to see whether they will pass on their superiority. When a superior sire is found he must be used again in order to obtain sons and daughters for use in breeding the next generation. The sons and daughters of a superior breeding animal must be similarly tested by progeny performance to determine those that transmit the desired qualities. This is especially difficult in beef cattle because animals on which the test is based have been slaughtered and the number of progeny from a female is limited. Suggestions for overcoming these difficulties are presented in the following section.[1]

TABLE 54.—PERFORMANCE RECORD OF FOUR CHOICE BEEF SHORTHORN STEERS*

Steer number	Days on feed	Daily gain, pounds	Feed to produce 400 lb. of gain	
			Grain, pounds	Hay, pounds
1	239	1.71	1,930	864
2	225	1.77	2,251	926
3	306	1.35	2,796	1,174
4	287	1.38	2,809	1,768

* KNAPP, B. JR., *Ext. Anim. Husbandman*, June, 1940.

It is obvious that steer No. 1 was a much more efficient converter of feed than was steer No. 4 in spite of the fact reported by Knapp that the No. 4 steer was the outstanding feeder type steer of the four.

Similarly Knapp reports differences between the progeny of different sires in the matter of efficiency of feed conversion.

[1] *U.S. Dept. Agr. Yearbook of Agriculture*, pp. 875–876, 1936.

TABLE 55.—PROGENY-PERFORMANCE RECORDS OF THE OFFSPRING OF SEVEN BULLS

Sire number	Breed	Average feed consumed by progeny to produce 100 lb. of gain	
		Grain, pounds	Hay, pounds
1	A	618	386
2	A	504	297
3	A	598	319
4	A	643	351
5	B	555	268
6	B	543	270
7	B	502	241

Again the progeny differences are evident, although we do not know whether to give all the credit or blame to the bulls because we do not know what the various dams' contributions were.

It is obvious from the above discussion that we want both good type and efficiency of feed conversion in our beef breeding animals and that both these things are to some, if not the full, extent hereditary. Being hereditary means that they are determined by genes so that we have a right to hope that, if means can be developed for measuring them, we will be able to create better type and more efficient animals through systems of breeding and selection. Several methods for determining record-of-performance merit have been proposed for beef cattle, and we have seen in some detail in Chap. XXIII the extended series of proposals for indexing dairy bulls that were made before a practical plan was devised.

A proposal by Holbert in 1932 was that of evaluating beef sires on the basis of the showyard winnings of their progeny. Although such factual data might have some value, it would also easily lend itself to unwarranted exploitation; and, because of its highly selected nature and its possible lack of a realistic genetic basis, it could not be expected to contribute a great deal to sound beef-cattle improvement. Sheets in 1932 proposed a record of performance for beef cattle based on feed consumption of calves from birth to slaughter or maturity, rate of daily gain, and a slaughter score based on dressing percentage and the physical and chemical characteristics of the cooked meat. Efficiency could be expressed by the number of pounds of cold dressed carcass produced per 100 lb. of total digestible nutrients consumed from birth to slaughter or maturity, and quality on the basis of carcass grade combined with a score for tenderness of cooked rib, the two being given relative weightings of 65 and 35 points, respectively, so that the final score would be

$$\text{Record of performance} = 0.05\,(E)(Q)$$

where E = gain per pound of total digestible nutrients fed and Q = carcass grade in percentage. The two scores used in arriving at this final score would be preserved in the record, for they are individually useful. This system is too complex for general use and has since been modified to fit practical conditions by Knapp, Black, and other workers in the Bureau of Animal Industry.

In 1933 Winters and McMahon at the University of Minnesota proposed a method of evaluating performance in beef cattle based on average daily gain from birth to one year of age and a quality score based on conformation at the end of one year.

Data on 147 steers located at three Bureau Animal Industry Experiment Stations were used by Black and Knapp to test the accuracy of the above methods of evaluating records of performance in beef animals. Analysis of variance studies with Sheets's proposal showed "a large amount of uncontrolled variation between calves by the same sire," and with the Winters and McMahon proposal it showed "less uncontrolled variance than using Sheets's proposal but still too large to show significant differences between sires."

As the work progressed at Beltsville and larger volumes of data became available for study, the need for further refinement in methods became evident. In studying the problem, the writers in 1936 made a correlation study of the data accumulated by the Bureau during the preceding 5 years. One correlation showed that there was no relationship between efficiency of gain during the suckling period and the efficiency of gain during the feeding period. It was logical to assume that there should be a relationship provided that the inherited factors influencing efficiency of gain during the life of the calf were active during both periods. This failure to obtain a significant correlation led us to believe that during one period or the other, uncontrolled variation resulted in this lack of correlation. It was, therefore, decided to adopt a period in which as many variables as possible could be controlled. A method was proposed based on efficiency of gain from 500 to 900 pounds and a quality score based on carcass grade. This method very closely parallels the method used by the Danish swine breeders in their outstanding work in testing performance in swine. When this method was also applied to the data from the three stations, the analysis showed that differences between sires were highly significant.

There are several points that we should consider in view of the above comparison. We have made this comparison solely on the basis of progeny performance. The methods of Sheets and Winters are so devised that selection would be made for heavy milking qualities provided either of these methods were applied as a means of phenotypic selection. Thus, under such selection, the milking qualities of the herd would reach a maximum level of production.

The method proposed by the writers, however, does not preclude emphasis on milk production, but we believe the results are perhaps less influenced by the milk production of the dam than they are in the case of the other two methods. It is the progeny we propose to test to determine the breeding ability of a par-

ticular sire as against that of another and the method used should eliminate as much nongenetic variation as possible.

In view of the above analysis, we believe this method offers a more accurate means of selection on the basis of progeny performance. It is recognized that this method is not the final word in measuring performance in beef cattle, and we are working at present on ways to develop a simpler and more practical method than we now have that will consistently demonstrate differences between sires.

Genotypic selection has been clearly demonstrated to be an effective means for improvement in animals as demonstrated by Reed with dairy cattle; by Lush with Danish swine, and by Goodale with albino mice. It is our belief that only by such selection will it be possible to bring about consistent improvement in cattle and it is toward this end that these studies are directed.[1]

The matter of measuring efficiency of gain as any beef animal gains from 500 to 900 lb. in weight is simply a procedure in weighing feed and keeping records. Because many people interested in this problem are not technically trained cattle graders, and because the Bureau of Animal Industry studies of data on steers had indicated a rather close association between height at the withers and weight, on the one hand, and slaughter grade, on the other, Knapp has by means of multiple curvilinear regressions, constructed tables whereby the height at withers and weight or heart girth of steers can be used to determine slaughter-grade classification as indicated in Tables 56 and 57 (next page).

The omission of weights at the end of each column (in Tables 56 and 57) giving the higher grades is explained by the fact that, as an animal acquires an excess of skeletal size, it becomes increasingly difficult for it to attain the degree of fatness required in the higher grades.[2]

It is seen from the above that a practical yardstick for measuring the efficiency of feed utilization and quality of finished product of a group of offspring by a bull is now available. When it is not convenient or possible to secure the actual efficiency of feed utilization, the work of Winters indicates that rate of gain can be safely substituted.

Gregory,[3] from an investigation of the nature of the growth factors in cattle, proposed as an index of the conformation of this class of livestock the muscle-skeleton index derived by dividing the round measurement (in inches or centimeters) taken from one patella around the rear of the animal to the other and parallel to the ground by the height at the withers (in inches or centimeters). If an animal gave a round measure-

[1] Black, W. H., and Knapp, B., Jr., A Comparison of Several Methods of Measuring Performance in Beef Cattle, *Amer. Soc. Anim. Prod. Proc.*, 1938, pp. 103–107.

[2] Knapp, B., Jr., Determination of Slaughter-steer Grades from Weights and Measurements, *U.S. Dept. Agr. Cir.* 524, May, 1939.

[3] Gregory, P. W., The Nature of Size Factors in Domestic Breeds of Cattle, *Genetics*, **18**: 221–250.

TABLE 56.—SLAUGHTER-GRADE CLASSIFICATION OF STEERS ON THE BASIS OF HEIGHT AT WITHERS AND WEIGHT*

Height of steers at withers, inches	Weight of steers that grade, pounds				
	Prime†	Choice	Good	Medium	Plain‡
38	701	606– 700	523– 605	452– 522	451
38½	719	622– 718	537– 621	464– 536	463
39	738	638– 737	552– 637	477– 551	476
39½	758	655– 757	566– 654	489– 565	488
40	778	672– 777	581– 671	502– 580	501
40½	798	690– 797	596– 689	516– 595	515
41	820	708– 819	612– 707	529– 611	528
41½	841	727– 840	628– 726	543– 627	542
42	863	746– 862	645– 745	558– 644	557
42½	886	766– 885	662– 765	572– 661	571
43	910	786– 909	680– 785	588– 679	587
43½	934	807– 933	698– 806	603– 697	602
44	959	829– 958	716– 828	619– 715	618
44½	984	851– 983	735– 850	635– 734	634
45	1,010	873–1,009	755– 872	652– 754	651
45½	1,037	896–1,036	775– 895	670– 774	669
46	1,064	920–1,063	795– 919	688– 794	687
46½	1,092	944–1,091	816– 943	706– 815	705
47	1,121	969–1,120	838– 968	724– 837	723
47½	1,151	995–1,150	860– 994	743– 859	742
48	1,181	1,021–1,180	883–1,020	763– 882	762
48½	1,213	1,047–1,212	906–1,046	783– 905	782
49	1,245	1,074–1,244	930–1,073	804– 929	803
49½	1,278	1,104–1,277	955–1,103	825– 954	824
50	1,312	1,134–1,311	980–1,133	847– 979	846
50½	1,346	1,164–1,345	1,006–1,163	869–1,005	868
51	1,382	1,195–1,381	1,033–1,194	892–1,032	891
51½	1,419	1,226–1,418	1,060–1,225	916–1,059	915
52	1,456	1,259–1,455	1,088–1,258	940–1,087	939
52½	§	1,292 or more	1,117–1,291	956–1,116	964
53	.....	1,326 or more	1,146–1,325	991–1,145	990
53½	.....	1,361 or more	1,177–1,360	1,017–1,176	1,016
54	.....	1,397 or more	1,208–1,396	1,044–1,207	1,043
54½	.....	1,434 or more	1,240–1,433	1,072–1,239	1,071
55	.....	1,472 or more	1,272–1,471	1,100–1,271	1,099
55½	.....	§	1,306 or more	1,129–1,305	1,128
56	.....	....	1,341 or more	1,159–1,340	1,158
56½	.....	....	1,376 or more	1,190–1,375	1,189
57	.....	....	1,413 or more	1,221–1,412	1,220
57½	.....	....	1,450 or more	1,253–1,449	1,252
58	.....	....	1,489 or more	1,287–1,488	1,286
58½	.....	....	§	1,321 or more	1,320
59	.....	....	....	1,356 or more	1,355
59½	.....	....	....	1,392 or more	1,391
60	.....	....	....	1,428 or more	1,427

* *U.S. Dept. Agr. Cir.* 524, May, 1939.
† Minimum weight.
‡ Maximum weight.
§ Omission of weights explained in text

TABLE 57.—SLAUGHTER-GRADE CLASSIFICATION OF STEERS ON THE BASIS OF HEIGHT AT WITHERS AND HEART GIRTH*

Height of steers at withers, inches	Heart girth of steers that grade, inches				
	Prime†	Choice	Good	Medium	Plain‡
38	64¾	60½–64½	56½–60¼	52¾–56¼	52½
38½	65½	61¼–65¼	57 –61	53¼–56¾	53
39	66	61¾–65¾	57¾–61½	54 –57½	53¾
39½	66½	62¼–66¼	58¼–62	54½–58	54¼
40	67¼	63 –67	59 –62¾	55 –58¾	54¾
40½	68	63¾–67¾	59½–63½	55½–59¼	55¼
41	68¾	64¼–68½	60 –64	56 –59¾	55¾
41½	69½	64¾–69¼	60½–64½	56¾–60½	56½
42	70	65½–69¾	61¼–65¼	57¼–61	57
42½	70¾	66¼–70½	62 –66	57¾–61¾	57½
43	71½	66¾–71¼	62½–66½	58¼–62¼	58
43½	72¼	67½–72	63¼–67¼	59 –63	58¾
44	73	68¼–72¾	63¾–68	59½–63½	59¼
44½	73¾	69 –73½	64½–68¾	60¼–64¼	60
45	74½	69¾–74¼	65 –69½	60¾–64¾	60½
45½	75¼	70¼–75	65¾–70	61½–65½	61¼
46	76	71 –75¾	66½–70¾	62 –66¼	61¾
46½	76¾	71¾–76½	67 –71½	62¾–66¾	62½
47	77½	72½–77¼	67¾–72¼	63¼–67½	63
47½	78½	73¼–78¼	68½–73	64 –68¼	63¾
48	79¼	74 –79	69¼–73¾	64½–69	64¼
48½	80	74¾–79¾	70 –74½	65¼–69¾	65
49	81	75½–80¾	70½–75¼	66 –70¼	65¾
49½	81¾	76¼–81½	71¼–76	66¾–71	66½
50	82½	77¼–82¼	72 –77	67¼–71¾	67
50½	83½	78 –83¼	72¾–77¾	68 –72½	67¾
51	84¼	78¾–84	73½–78½	68¾–73¼	68½
51½	85¼	79½–85	74¼–79¼	69½–74	69¼
52	86	80½–85¾	75 –80¼	70¼–74¾	70
52½	§	81½ or more	76 –81¼	71 –75¾	70¾
53	....	82¼ or more	76¾–82	71¾–76½	71½
53½	....	83 or more	77½–83¾	72½–77¼	72¼
54	....	84 or more	78½–83¾	73¼–78¼	73
54½	....	84¾ or more	79¼–84½	74 –79	73¾
55	....	85¾ or more	80 –85½	74¾–79¾	74½
55½	....	§	81 or more	75½–80¾	75¼
56	....	....	81¾ or more	76¼–81½	76
56½	....	....	82¾ or more	77¼–82½	77
57	....	....	83½ or more	78 –83¼	77¾
57½	....	....	84½ or more	78¾–84¼	78½
58	....	....	85½ or more	79¾–85¼	79½
58½	....	....	§	80½ or more	80¼
59	....	....	....	81½ or more	81¼
59½	....	....	....	82½ or more	82¼
60	....	....	....	83¼ or more	83

* *U.S. Dept. Agr. Cir.* 524, May, 1939.

† Minimum measurement.

‡ Maximum measurement.

§ Omission of measurements explained in text.

ment of 106 cm. and a height at withers of 123 cm., the index RM/H would be 862. This would be a rather typical, low-set, well-muscled beef type. A dairy-type animal, on the other hand, might give a round measurement of say 90 cm. and a height at withers of 126 cm. or muscle-skeleton index of 715. Gregory found that the dividing line in general between beef and dairy-type animals of several breeds and all ages came at index 785. Since the index for beef animals remains relatively constant from birth on, this objective measure might be made to serve a useful selective function. The round measure for this group of animals showed a high correlation with weight ($r = .875 \pm .017$) and a low correlation with height at withers ($r = .190 \pm .072$), while the correlation between height and weight was intermediate ($r = .383 \pm .064$).

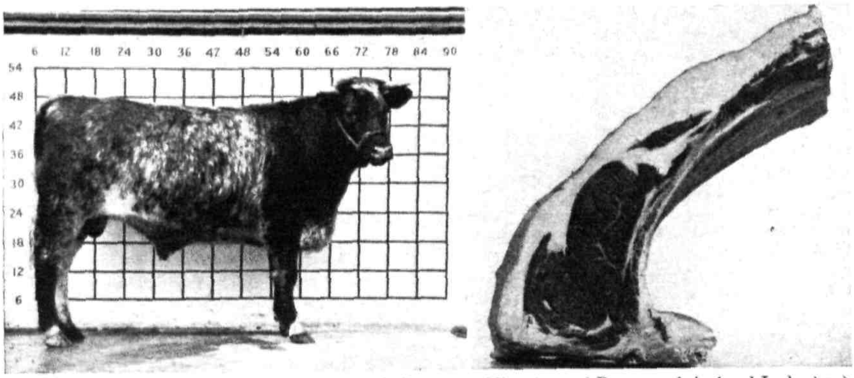

FIG. 193.—Beef-type Shorthorn steer and rib cut. *(Courtesy of Bureau of Animal Industry.)*

The following is a recent proposal regarding record-of-performance procedure with beef cattle.

Introduction.—Much progress has been made by beef-cattle breeders in fixing type and conformation. For the very important factor of efficiency of feed utilization, however, much less progress has been made. This is due largely to the lack of adequate methods for measuring this characteristic, although it has been generally recognized that much variation exists in cattle in this respect. In the past few years a considerable amount of research has been done on this subject, and certain methods have been devised that can be used in evaluating differences in efficiency. While such research is yet in its infancy, certain of the methods developed should be helpful to the breeder in producing more efficient cattle.

Purpose.—The objective of these recommendations is to aid breeders in developing more efficient strains of beef cattle. The information gathered should aid in the appraisal of the performance of sires, dams, and offspring.

GENERAL PRINCIPLES

1. From birth to weaning all calves in any one herd will be fed alike within reasonable limits as far as possible without extra expense.

2. Females that do not produce enough milk to feed their own calves will be culled.

3. No male calf whose dam does not give sufficient milk for his development will be saved for breeding purposes.

4. Young stock will be handled similarly as to housing and grazing.

5. Young stock will be scored at a standard age or weight. The recommended time of scoring will necessarily differ, dependent upon the environmental conditions under which the animals are raised.

Detailed Recordings and Procedure

1. Individual number for each animal.
2. Pedigree.
3. Weight at birth.
4. Weaning weight and age.

(*a*) Under farm conditions where beef production is intensive calves will be weaned on a weight basis, the weights being as close to 450 pounds for heifers and 500 pounds for bulls or steers as is possible.

(*b*) Under most range conditions it will be impossible to bring each calf to a standard weight or age before weaning. The optimum age of weaning will vary under different range conditions. It may even become desirable under certain conditions to alter weaning age somewhat from year to year. Changes in age of weaning are not desirable but will not be serious if the calves of any one crop are treated alike. As a general policy it is recommended that range calves be weaned at an average age of 5½ months. In most cases it will be necessary to wean groups of calves when the average age is about 5½ months or whatever age is set as standard for that herd.

5. Standard post-weaning treatment.

(*a*) In herds being developed under farm conditions the calves should be placed on *full* feed after weaning. Standard rations should be used; they may vary for different sections of the country. Rations should consist of those feeds common to the area and should contain (1) a cereal grain, (2) a protein supplement, and (3) a good-quality roughage. The cereal grain may consist of corn, wheat, barley, oats, rye, grain sorghums, rice, or any combination of these grains. The protein supplement should be limited to cottonseed meal, linseed meal, soybean meal, peanut meal, or velvet-bean meal. The roughages should consist of any good-quality hay or silage available at the feed lots. In areas where it is known that mineral deficiencies exist, suitable mineral supplements for correcting such deficiencies should be provided. Salt should be available at all times.

The individual feeding of each calf is recommended wherever possible and in order to make comparisons between individuals it is necessary that the calves be fed under as nearly similar conditions as possible. Differences in weight during the feeding trial affect efficiency of feed utilization and for this reason it is recommended that the following weights be used for the test feeding period:

Heifers: 450 to 850 pounds
Males: 500 to 900 pounds

Where individual feeding is used, a record will be made of the feed consumed by each calf.

In many herds it may not be possible to carry out an individual feeding program. This would apply to large farms or ranches where several bulls may be used each year and a test on each bull is desired. In these cases, the calves by any one sire may be fed as a group for a period of not less than 6 months. The weights of the calves in any one group will naturally be variable but the ages should not vary more than the 45 days. Rate of gain of each animal during the feeding period will give a very useful guide as to relative efficiency of each calf since rate of gain is closely related to efficiency of feed utilization; *i.e.*, the fast-gaining animal is likely to be the efficient animal. Records should be kept of the amount of feed consumed by each lot.

(*b*) Under range conditions it may be more useful to test heifers under environmental conditions comparable to those prevailing for the remainder of the breeding herd. In this case it is recommended that the heifers be weighed when approximately 12 and 18 months old and scored when 18 months old.

6. Every animal within any one group will be scored at the same end point—weight or age. Calves that are placed on full feed will be scored at the close of the feed-lot trial. Calves retained for breeding that are reared under range conditions will be scored when about 18 months old; this will be at about the close of the second grazing period.

Any scoring system by which it is possible to record the individual merit of each calf will be satisfactory. A system similar to that described on A.H. Form 522 or a scoring plan based on measurements as presented in *U.S.D.A. Circular* No. 524 may be used.

7. The following items will be recorded for each calf:

Summary

Animal No._______ Sex_______ Birth date_________ Birth weight_____
Sire__________________ Dam__________________

Performance Record

Birth to weaning		After weaning	
Date weaned........	________	Date finished........	________
Age at weaning......	________	Age................	________
Weight at weaning...	________	Final weight........	________
Total gain...........	________	Total gain..........	________
Daily gain...........	________	Daily gain..........	________
Score at weaning.....	________	Feed per 100 lb. gain (list each feed)....	________
		Score at end of test..	________

PERFORMANCE DATA

1. The final evaluation of the individual calf will be based on the following performance data:

(*a*) Gain during nursing period.
(*b*) Gain during feeding period.
(*c*) Feed per 100 lb. gain (if available).
(*d*) Score.

2. The evaluation of the female as a dam will be based on her calves' performance as outlined above with possible added emphasis given to the calves' gain during the nursing period.

3. The evaluation of the sire will be based largely upon his calves' performance in—

(*a*) Gain during the feeding period after weaning.
(*b*) Feed per 100 lb. gain (if available).
(*c*) Score per 100 lb. gain (if available).[1]

There remains, however, one further problem to be solved before we can have a performance index on a beef bull comparable with the index used with dairy cattle. This arises from the fact that all the offspring of any bull receive half their inheritance from their dams. In other

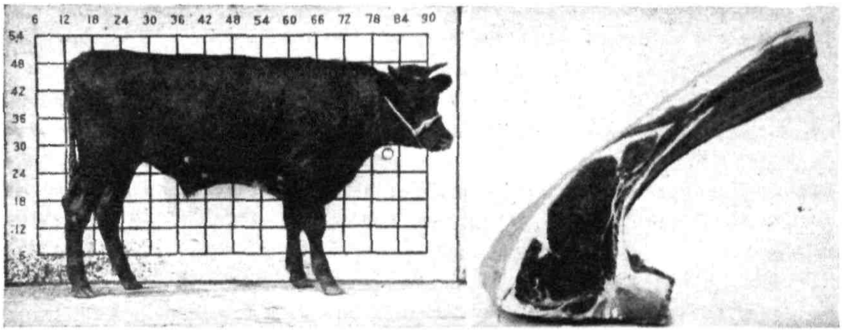

FIG. 194.—Dual-purpose Shorthorn steer and rib cut. (*Courtesy of Bureau of Animal Industry.*)

words, we should, ideally, formulate the bull's index on the basis of a comparison of the dams' and their offspring's performance as is done in indexing dairy bulls. The daughters of high-producing dairy cows produce more milk than their half sisters out of poor-producing cows, and observation indicates that the same general principle holds in beef animals.

Since the feeding practices for fattening steers and for developing breeding heifers are so different, some sort of correction factors must be worked out so that they can be compared, just as the dairy breeder uses age and other correction factors. This would mean using rate of gains for certain periods of time in arriving at the feed utilization efficiency of a group of cows and also the use of live-animal grades in place of slaughter grade for the cows.

[1] Prepared by Bureau of Animal Industry beef-cattle specialists in cooperation with the Minnesota Agricultural Experiment Station. Acknowledgment is made also to the agricultural experiment stations of Indiana, Iowa, and Montana for their valuable assistance. *U.S. Dept. Agr., Bur. Anim. Indus., Anim. Husb. Div.* No. 37, March, 1941.

It is seen, therefore, that there are many practical difficulties attending the compilation and interpretation of data on which a genetically sound progeny-performance index for beef cattle can be based. The fact that genetic differences in efficient beef production exist among our animals, however, has been so abundantly demonstrated that we are forced to conclude that no rapid progress in breeding better beef animals is likely to ensue until record keeping has yielded a fund of information regarding performance and quality, so that pedigrees with relevant data can be written to aid the breeder in choosing between equally desirable animals as far as their phenotypes are concerned. Such complete pedigrees will be of inestimable value in selecting sires, and the records necessary in progeny-performance testing can be utilized by each breeder to ascertain the best female lines in his own herd.

Selection Indexes in Dual-purpose Cattle.—Because dual-purpose cattle are kept both for milk and beef production, it is obvious that breeders should use both the index commonly in use in dairy herds (see Chap. XXIII) as well as the one now in process of formation for beef animals. The problem here is similar to that found in all classes of livestock, *viz.*, the securing of sufficient data so that selection may be practiced in keeping with the known laws of inheritance, in other words that it rest on a sound genetic basis.

Dual-purpose cattle selection is not very different from that prevailing in all other classes of livestock, for most breeders try to select for more than one thing at a time. Here we are selecting for two major things at once, milk and beef, and in addition the two things are to some degree antagonistic. We know, therefore, at the start that we will probably never combine both things in their extreme degrees in any one animal. The beef breeds have many genes for beef production and a few for milk production owing to the breeding and selection that has been practiced in the past. The opposite situation, of course, prevails in the dairy breeds. Dual-purpose cattle breeders want about a 50–50 combination of beef and milk genes. Discovering the animals that come closest to having such a genetic make-up by testing and record keeping followed by intelligent mating and the use of some degree of inbreeding should eventually produce strains of animals that are relatively pure for the qualities desired, although there will always be considerable nonhereditary variation and in the very nature of the case probably more genetic variation than found in comparable situations involving only beef or only milk.

Selection Indexes in Sheep.—In colonial America, sheep were grown almost entirely for the purpose of producing wool. This led shortly to the creation, from Spanish Merino importations, of the American Merino breed, which became very numerous along the Eastern seaboard

with Vermont at that time the leading state in number of sheep, owing in large measure to the influence of William Jarvis, who had a farm at Weathersfield, Vt., and at the time was serving as American consul in Lisbon, Portugal. The wool clip in the early colonies was only 2 or 3 lb. per animal per year, but through selection it has been continuously raised to an average level of 7 or 8 lb. for the present sheep population (all types) of the United States.

From the Vermont Merino, there were later developed the various Delaine Merinos for the purpose of producing a fine wool of sufficient length for combing. Most of the numerous Merino breed associations that had sprung up were merged in 1906 into the American and Delaine Merino Record Association with three other smaller associations still existing. Merino type varies from a small thin animal of poor carcass quality but heavily wrinkled and producing a fine, dense, heavy fleece of short wool (Type A), to a larger, fairly heavy, and low-set animal producing a good carcass but generally lacking wrinkles (except on the neck) and with a heavier but less fine and dense fleece (Type C or Delaine), and a third intermediate form (Type B).

From Spanish Merino foundations, the French developed a fine-wool strain of sheep, the Rambouillet, of much greater size than the American Merino. Many of these animals were brought to America about the middle of the nineteenth century and for a time they were a very popular breed. Interest then declined, to be revived about 1890. The Rambouillet is a large animal producing a heavy, dense fleece. As with the American Merino, there are variations in amount of skin wrinkles and at some shows the animals are divided into B and C types, which correspond closely to the similar types in the American Merino. They were brought to America to serve primarily as wool producers. In recent years, greater attention has been paid to fleshing qualities, more by some breeders than others, but the carcasses are not of as high a grade generally as those from the Down breeds. This breed has been called the most typical dual-purpose breed in America, yielding something in density and fineness of fleece to the American Merino and to the Down breeds in quality of carcass. Under these conditions, we would expect to find wide degrees of variation in the breed.

Robert Bakewell, the noted English livestock breeder of the eighteenth century, greatly improved one of the long-wool breeds, *viz.*, the Leicester. He devoted his major attention to fleshing or fattening qualities and quite neglected consideration of wool. The result was a fairly large breed of sheep with rather long and coarse wool and a carcass of a coarse grain, which when finished was overlaid with several inches of fat. To a greater or less extent, these qualities are found also in the other long-wool breeds, Cotswolds, Lincolns, and Romneys. The long-wool breeds

were created, therefore, primarily to serve as meat animals supplying the large, fat legs and roasts then in demand. In recent years, more attention has been paid to wool and attempts have continually been made to improve the quality of carcass. The fine-wool breeds generally pay particular attention to fleece, less to carcass qualities. The long-wool breeds on the other hand pay more attention to carcass, less to fleece.

The various "Down breeds" of sheep, Southdowns, Shropshires, Oxfords, Hampshires, etc., have been developed to fill the void between

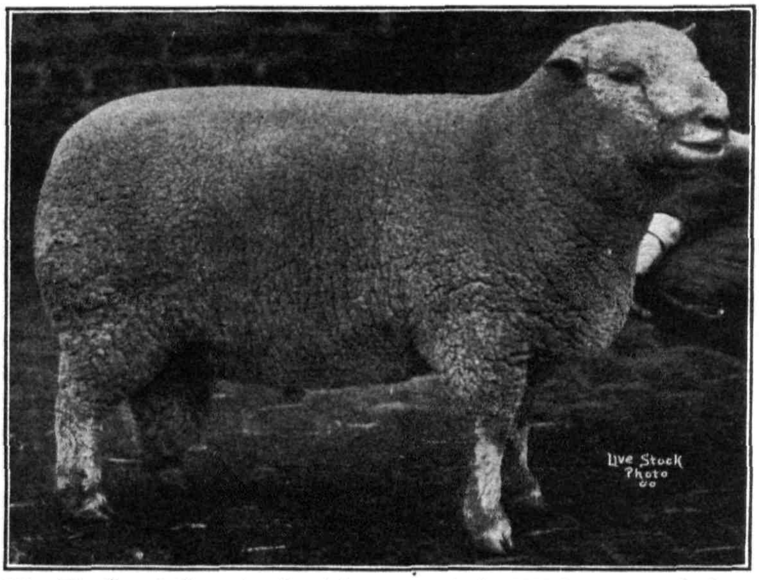

FIG. 195.—The Grand Champion Southdown ram at the 1925 International, shown by Mountain Farm, Bradstreet, Mass.

the fine-wool and long-wool breeds. They have neither the fine quality nor weight of wool found in the fine wools nor the amount of meat found in the long-wool breeds. They are, in a sense, a happy medium between two extremes with the very great added advantage of producing very superior carcasses from the standpoint of quality. The various Merinos and the Down breeds have been bred and kept relatively pure in the East and Midwest. In the range country farther west, the foundation females were largely grade Rambouillet ewes. On these ewes, there have been used all the types of American and Delaine Merinos and Rambouillet rams. Later, rams from the long-wool breeds were used, particularly Cotswolds and Lincolns, in the attempt to improve size and fleshing, and rams from the Down breeds were used to try to improve carcass quality still further. Finally the use of long-wool rams on Merino

ewes in the attempt to get good sheep from the standpoint of both wool and mutton led to the formation of the Corriedale breed in New Zealand (imported to the United States in 1914) and the Columbia, Panama, and Romeldale breeds in the United States. At the Bureau of Animal Industry experimental farm in Middlebury, Vt., a new breed, the Southdale, is now in process of formation through the crossing of Corriedales and Southdowns.

As will be seen from the above discussion, there are a great many types of sheep that have been developed to suit the needs of various markets and environments. In general, the sheep breeder has a dual aim. He must produce fairly meaty lambs of good carcass quality, and at the same time his ewes must produce enough good-quality wool to pay for their yearly cost of keep. He wants as many pounds of lamb per 100 lb. of ewe as he can get plus a heavy, uniform, high-quality fleece. He must pay attention to prolificacy, ease of lambing, milking ability, and natural fleshing. As with dual-purpose cattle, some of these qualities are more or less antithetical. If he gets too great propensities for wool production and milking ability, natural fleshing is apt to suffer, and vice versa. In addition he must pay attention to general vigor and longevity, for susceptibility to diseases or parasites or too rapid turnover of the flock both reduces immediate profit and lessens the effectiveness of selection.

Finally, breed trade-marks must receive attention from purebred breeders—short ears here, medium or long there; face and leg coverings and colors of various degrees and shades. Unfortunately, the sort of face covering necessary to win in the show ring may render an animal partly or totally blind, so that good feeding and growth in the feed lot or on the range is impossible. In the show ring, sheep are trimmed so that no estimate of their yearly wool growth is possible, and still there is enough wool there to make the judgment of carcass development and quality difficult. Show-ring type generally calls for a short body, which is probably more or less negatively correlated with prolificacy. A well-known sheep breeder once remarked that he had "never owned a great sire that could win in the show ring," though this need not necessarily be so.

With so many factors involved and with the animals themselves probably in most instances quite heterozygous, the sheep breeder's problem is anything but a sinecure. As with all other classes of livestock, the problem in sheep breeding has two phases, one to discover by record keeping what qualities our animals now possess and in what degree, and the other to bring together these revealed desirable qualities in our animals of the future and to render them relatively homozygous through judicious line- and closebreeding.

If a man were breeding for nothing but wool, it would be a relatively simple matter to work out an index for rams on the basis of a comparison between ewes and their offspring's amount and quality of wool clip, just as the dairy-cattle breeder secures a bull index by comparing daughters' and dams' yearly production of milk and butterfat test. We would need correction factors for different ages and perhaps for the sexes, and since wool production, like milk production, is greatly influenced by the environment, we know that an average of several years' production is a safer estimate of an animal's inheritance than is that of any one year.

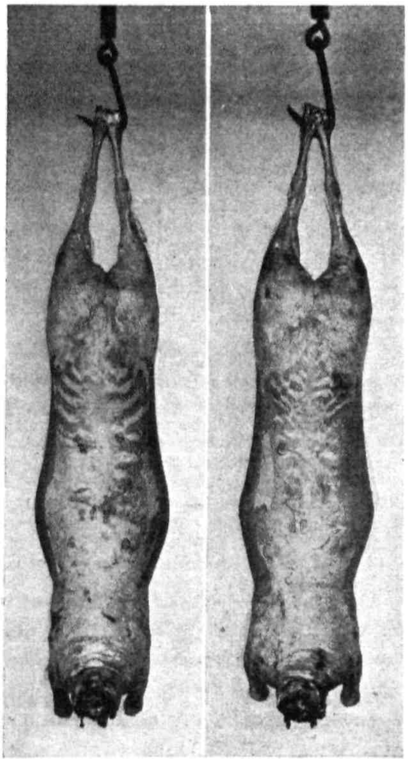

FIG. 196.—Different types in lamb carcasses. (*Courtesy of Bur. Anim. Indus.*)

Likewise, if a man were breeding for nothing but carcass quality, he would need a ram index based upon a comparison of rate of gain and carcass quality between the ewes and their offspring.

Since most sheep breeders desire as much efficiently produced and high-quality lamb carcass per 100 lb. of ewe maintained and as large an amount of high-quality wool as possible from their ewes each year, a record of performance for sheep should include both these items. With differences in age, sex, type of birth (singles, twins, etc.), and time of shearing properly standardized, and with environmental conditions held as constant as possible or corrected to a standard basis, it should be possible to work out a system for indexing rams on the basis of a comparison between their mates' and their offsprings' performance in producing both wool and meat.

Christgau of the University of Minnesota has proposed a record of performance for sheep based on the amount and quality (grade-corrected) of lamb produced per 100 lb. of ewe maintained, with the wool production (grade-corrected) converted on a relative price basis to its equivalent in pounds of lamb. In place of individual feed records on lambs, the rate of gain per unit of feed maintenance (varying to the 0.73 power of the weight for mature animals and to the 0.64 power in growing animals)

is suggested as the measure of relative efficiency of gain. Christgau suggests the following standardized plan of records and management:

1. Record the ewe's weights, breeding dates and fleece weights and grades.
2. Shear at the same time each year, and weigh ewes each year at shearing time and breeding time.
3. Record the lambing dates and lambs' weights.
4. Stamp the ewes' and lambs' numbers on the side of the body, using a system avoiding annual duplication. Stamp lambs at birth, and ewes at shearing.
5. Wean and weigh to the nearest pound each ewe's lambs when 15 weeks old.
6. Weigh each ewe's lambs when 23 weeks old.
7. Standardize as nearly as possible all feeding, breeding, and management practices.

These records to be kept on an individual ewe card for tabulation of a lifetime performance record which will enable the breeder to identify the most efficient individuals in the flock.[1]

There are many knotty problems involved in the progeny testing of rams. In the first place, we are generally selecting for more than one major item; *viz.*,, mutton and wool besides a number of others such as type, fertility, longevity, transmitting ability, etc., and, for any and all of these, we at present lack yardsticks of measurement to say nothing of a general yardstick that would include all of them. In addition, sheep reproduce at a low rate compared with fruit flies or corn, and the records cost considerable in time, effort, and money. Finally, we do not yet know how to evaluate properly many environmental influences, and, until this can be done, our selection is unlikely to rest on a firm genetic basis. Amount of wool produced is greatly influenced by temperatures, nutrition, and other environmental conditions. Size of lamb at weaning is influenced by its sex, its type of birth, time of birth, and the condition and milking quality of its dam. It is obvious, therefore, that corrections must be applied to these various features before we can distinguish the breeding or transmitting merit of rams.

Lambs born as singles, those which are larger at birth, and those born early in the lambing season will generally be larger at weaning than those born in multiple births, those that are small at birth, or that are born late, so that if we practice selection at weaning the former sorts of lambs will have a decided advantage that might or might not be associated with a better genetic complex. Since the number of young born at a time and the time of heat are at least in part genetic, *i.e.* based on the inherent functioning of a ewe's ovaries, selecting the biggest and best lambs at weaning might give us a flock that would tend to breed early but also one in which

[1] CHRISTGAU, R. J., A Record of Performance for Sheep, *Amer. Soc. Anim. Prod. Proc.*, 1939, pp. 342–347.

few twins would be born. Chapman and Lush have shown that about 25 to 30 per cent of the variance in the birth weights of lambs is due to inheritance, 30 to 35 per cent to tangible environmental effects, and 40 to 45 per cent to intangible environment or accidents of development.

A study of the lambs born during the 14-year period (1921–1934) in the Hampshire, Shropshire, and Southdown flocks at the National Agricultural Research Center at Beltsville, Md., has shown by statistical analysis that for this population with selection beginning to be practiced at three months of age there is a tendency

1. To select lambs born as singles over those born as twins.
2. To select those born early over those born late.
3. To select those which were heavier at birth.

From these results it is evident that lambs born as singles or early in the season or that were heavy at birth tended to be favored in selection. From a genetic standpoint this result reduces the chances of selecting animals that are superior in mutton form, since there is no apparent reason to assume that any one of these groups should have more desirable genes for mutton qualities than any other group. The favoring of singles might also be interpreted as selection against the trait of twinning. This is not necessarily so, however, since if only half as large a proportion of twins as of singles is retained, dams producing those single and twin lambs will be represented equally in the offspring retained for breeding.[1]

This study also showed that there was a tendency for differences in weight due to type of birth, to time of birth, and the weight at birth to disappear as the animals matured, whereas differences due to sex tended to be retained or increased.

The results showed that type of birth, time of birth, and birth weight have influenced the selection of breeding animals. Single lambs have been preferred to twins, early lambs to late ones, and lambs that were heavy at birth to light lambs. With the exception of a portion of the effect of birth weight, the effects of these factors on selection are considered to be environmental in nature, and, therefore, reduce the chances of selecting the genetically superior animals for breeding purposes. This weakness in the present method of selection can be at least partly overcome in one of the following ways:

1. When selections are made at weaning or a similar early age, the animals may be divided, first by sex and then into single and twin groups within sexes. These last two groups should then be divided according to time of birth. If the range in date of birth is 6 weeks, the lambs may be divided into two groups having a range of 3 weeks each. If lambing occurs over a longer period, more groups may be necessary. With the animals so divided, those in each group will be on a more comparable basis than if considered as a whole, and selections can be made within each group. This division does not take into consideration

[1] PHILLIPS, R. W., and DAWSON, W. M., Some Factors Affecting Survival, Growth and Selection of Lambs, *U.S. Dept. Agr. Cir.* 538, 1940.

differences in birth weight, and if data on this point are available they may be kept at hand for use while making selections. Selections would, of course, be based on the characters in which the breeder is primarily interested, such as mutton form, fleece, and perhaps other factors such as pedigrees of the animals.

This method eliminates comparison of single lambs with twin lambs and of early lambs with late ones. Assuming that the proportion of individuals possessing superior germ plasm is equal in the groups of singles and twins and that there is a similar proportion in the early and late group in each type of birth, the chances of actually selecting these superior animals would be greater if this suggested system was followed.

2. Selection may be made at a standard age, such as 6 months, rather than on a certain date. Weights at this age could be adjusted for the effects of birth factors, and any advantage or disadvantage kept in mind when evaluating each animal. The weights of all animals could be adjusted to a standard basis, such as single males of a standard birth date and weight, for use in making such allowances for the effects of birth factors and sex. All animals reaching the standard age within a given week might be observed on one day during that week. By this method each individual is compared with an ideal at a standard age, with allowance for any unfavorable environment due to birth factors. The effect on selection would be similar to that of the first suggested method.

3. Selections might be postponed until an age when the effects of the birth factors on development discussed herein have disappeared. Little effect of type and time of birth and birth weight on development, as measured by weight, remains at 12 months. Retention of all animals to this age is not practical for the sheep breeder who must sell his discarded lambs when they reach market weight, but it may be a worthwhile procedure in experimental breeding, unless data taken at younger ages can be shown to be sufficiently representative of the animals' potential development.

Another application of the results of the study presented herein is in the comparing of groups of animals, such as the offspring of two or more rams in progeny testing. If the number of offspring from each of two rams is sufficiently large that practically equal numbers of singles and twins, lambs of heavy and light birth weights, and males and females are available, and if the time of birth of the lambs is comparable, then a comparison of the uncorrected weights of the two groups at a standard age would be valid. However, most young rams are tested on a small number of ewes. If the resulting small number of offspring of a ram are to be compared with those of another ram at an age when the effects of birth factors still persist, the figures given in this circular, or similar figures, can be used in making necessary adjustments. Adjustments for sex can be made in like manner. All animals might be adjusted to a basis of male singles with date of birth and birth weight constant.[1]

Studies[2] on sheep maintained at the U.S. Regional Sheep Breeding Laboratory at Dubois, Idaho, have shown that there are significant

[1] *Ibid.*

[2] Phillips, R. W., Schott, R. G., Lambert, W. F., and Brier, G. W., Some Factors Affecting the Progeny Testing of Rams, *U.S. Dept. Agr. Cir.* 540, 1940.

differences between years in the body weights, fleece weights, and fleece lengths of the fourteen-month-old female offspring of some 11 Columbia, 17 Corriedale, and 17 Rambouillet rams, each with 20 or more female offspring. These studies also showed correlations between dams and daughters of the Corriedale and Rambouillet rams ranging from −0.04 to +0.42, with 4 highly significant and 7 significant out of 24 for body weight; from +0.01 to +0.51, with 6 highly significant and 5 significant out of 24 for fleece weight; and from +0.02 to +0.50 with 10 highly significant and 4 significant out of 24 for length of fleece. Since the average coefficients were positive but small, it is assumed that heredity of the dams accounts for only a small part of the variation of their daughters. Since these rams were selected to the extent of having left at least 20 female offspring in the flocks, less variation would be expected among their progeny than if they had not been selected, thus significant or highly significant differences were found in only 20 of the 72 ram comparisons made (3 items × 2 breeds × 12 years' records = 72).

It is interesting that some differences were present among these selected rams, and much greater differences would be expected among untried and therefore unselected rams. If rams are to be tested on the basis of their progeny alone, it would be well to mate them to groups of ewes that have similar means and variability for the characters being tested. If this is done and the rams are bred to, say, 20 ewes, the offspring of each ram can be arranged in a frequency graph for each of the characters studied that enables one to see at a glance the range of each ram's offspring, and the mean or average of each ram's offspring in each regard can easily be ascertained. Thus the best ram in each regard or in a combination of two or all three (body weight, fleece weight, and fleece length) stands revealed. If the breeder desires to select for more than these three things, *i.e.*, to add type, strength of back, plumpness of leg, etc., he can do so provided he sets up objective measures of these things so that they too can be graphed. It should be obvious that the greater number of things which we select for at any one time both cuts down our likelihood of being successful or, to put it another way, increases the number of compromises we must make, for we are not likely to find rams whose progeny excel in all respects.

McMahon,[1] using the technique of analysis of variance in a study of medullation in New Zealand sheep, found that 40 per cent of the variation was due to year-to-year variation, and that the parents controlled only about 10 per cent of the variation shown by their offspring, "the remainder being due to complicated interactions of genetic effects, accidents of development and the effects of feeding and environment." Similar

[1] McMahon, P. R., *Proc. 9th Ann. Mtg. Sheep Farmers, Massey Agr. Col., Palmerston, New Zeal.*, 1940.

results were secured when fleece weights were studied, and preliminary studies have indicated that the same situation may prevail for body conformation or, in brief, as phrased by McMahon, "half the breeding goes down the throat."

If the parents control only 10 per cent of the economically important characters of sheep, then only one-tenth of the improvement we make by culling will be passed on to the progeny.

The importance of this becomes obvious when we illustrate with reference to some given characteristic such as fleece weight. Supposing that we cull 50 per cent of our ewes for low fleece weight—this will put up the average production of the remainder for about 0.8 lbs. If we use only average rams on these ewes the offspring will only be 0.04 lbs. better than they would have been if we had not culled for fleece weight at all. We would have to continue for 48 years, completely replacing our flock every two years, in order to get an improvement of 1 lb. in fleece weight in our flock and flock numbers could not be maintained. Very similar results could be shown for hairiness or for general all-round excellence of body or fleece.

It is very evident that culling to the extent of 50 per cent, which is all that the average man can afford to do in his young ewes, does not give any appreciable permanent improvement in the flock. Nearly 95 per cent of the improvement vanishes when the selected ewes die or are cast for age.

TABLE 58.—RATES OF IMPROVEMENT THROUGH SELECTION AND TESTING*

Method of selection	Percentage culled	Progeny improved	Relative generations for 1-lb. improvement	Relative time for 1-lb. improvement, years
Ordinary selection:				
Culling ewes only	50	0.042	24	96
Culling rams only	97	0.112	9	36
Culling rams and ewes	97 50	0.162	6.2	24
Utilizing progeny-tested sires:				
Progeny-test 20% rams at random, keep the best 3%		0.75	1.33	4
Culling 50% ewes; progeny-test 20% rams, keep 3%		0.79	1.26	4
Culling 80% rams; progeny-test 20% rams, keep 3%		0.82	1.22	4
Culling 80% rams and 50% ewes; progeny-test 20% rams, keep 3%		0.86	1.16	4

* McMAHON, P. R. *Proc. 9th Ann. Mtg. Sheep Farmers, Massey Agr. Col., Palmerston, New Zeal.,* 1940.

In the case of rams the situation is much better because culling can be so very much more stringent. We have only to keep about 3 per cent of our rams for replacement, and naturally the best 3 per cent of our rams will be so much above the average of the flock that, even although we only realize one-tenth of this difference in the offspring, the improvement will be a useful one. To illustrate from fleece weight again, for comparison, if we cull 50 per cent of our ewes and 97 per cent of our rams, we get an average improvement of 1.62 lbs., of which the progeny will show one-tenth, or 0.16 lbs. In about six generations, or roughly twelve years, we could put up the average fleece weight by 1 lb.[1]

Since only one-tenth of the difference between an individual ewe and the flock will apparently be passed on to her offspring, the author (McMahon) suggests that the offspring alone serve as a measure of breeding performance of rams and that 7 offspring are a sufficient number to establish a ram's breeding worth. If 20 rams are progeny-tested, one-half of them will increase yield of wool on the average (in this population) 0.38 lb., whereas the best ram of the 10 will increase wool clip by 0.9 lb. and the average of the best 3 by 0.75 lb.

The relative rates of improvement are shown in the table on page 663.

In order to exploit the potentialities of progeny testing in sheep to the fullest possible extent, three things are necessary:

1. To determine at the earliest possible moment which rams will leave the best stock before incorporating them into the stud proper. Since seven progeny are sufficient to prove a sire, promising ram lambs can be mated without danger of injury. In the following season, when the time comes for serious mating of these rams as two-tooths, we are in a position to select the best ram on the basis of the offspring left.

2. We must use our top progeny-test ram to the fullest possible extent by hand service and artificial insemination.

3. The rams should be tried out with groups of daughters of different sires. "Nicking" is known to give important results in the dairy industry, and leading studmasters consider that it plays an equal part in sheep breeding.[2]

It is quite evident that, as time passes, statistical techniques are gradually undermining the assurance which once resided in our ability to practice wise selection among our animals on the basis of visual observation and personal judgment, which is not to say that those old tools were wholly bad but rather that they were not nearly so good as we once thought they were. Their use can and must now be supplemented with these newer techniques if we expect to speed up the program of improving our livestock.

[1] *Ibid.*

[2] McMahon, P. R. *Proc. 9th Ann. Mtg. Sheep Farmers, Massey Agr. Col., Palmerston, New Zeal.*, 1940.

A cooperative project to study performance in sheep was inaugurated in 1933 between the Bureau of Animal Industry and the Massachusetts State College Experiment Station. Its objects were to study the inherent capacity of sheep for efficient production of meat and wool and to develop a record of performance for sheep.

Flocks of Southdown and Shropshire sheep were used in this study and were maintained on good pasture for practically 6 months of the year (May 1 to Oct. 1) and fed a ration of 2 lb. of mixed hay, 2 lb. of carrots, and 1 lb. of a grain mixture consisting of 3 parts oats, 3 parts corn, 3 parts bran, and 1 part linseed-oil meal from Oct. 1 to May 1 each year.

During the early years of the experiment the ewes were weighed twice a month during the winter and once a month during the summer, the lambs weekly until one year of age. During the last two years, all animals have been weighed at monthly intervals.

The lambs were graded by three men on the form represented in Fig. 197 at 140 days and those slaughtered were graded on a similar form with color of fat substituted for pelt at time of slaughter.

TABLE 59.—RATINGS OF SIRES BASED ON COMPOSITE RATING OF OFFSPRING

Sire	Lambs				Yearling ewes			
	Weaning weight	Market grade	Type	Carcass grade	Circumference	Grease weight	Fineness	Mean rank
				Shropshire				
188	2	2	2	3	2	1	5	2.43
3938	4	3	4	1	4	3	3	3.14
4454	3	4	5	4	5	5	2	4.00
40N	5	5	3	5	3	4	1	3.71
852	1	1	1	2	1	2	4	1.71
				Southdown				
3071	1	1	3	6	1	2	8	3.14
1N	2	3	4	7	2	3	7	4.00
272	3	4	1	1	3	5	5	3.14
3063	4	5	6	3	5	1	6	4.29
172	6	8	5	4	4	4	4	5.00
22N	8	6	2	2	8	7	2	5.00
6P	5	7	7	5	6	6	3	5.57
112N	7	2	8	8	7	8	1	5.86

The retained yearling ewes were scored on the basis of the fineness, density, length, and weight of fleece and were measured for width and

A.H. Form 402
UNITED STATES DEPARTMENT OF AGRICULTURE
BUREAU OF ANIMAL INDUSTRY

Lot no.______________ Breed______________ Date______________
Individual no.______________ Station______________ Where graded______________

Item	AA1	Prime			Choice			Good			Medium			Common			Cull		
		A1+	A1	A1−	1+	1	1−	2+	2	2−	3+	3	3−	4+	4	4−	5+	5	5−
	1	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32	34	36
Width of body,		Very wide				Wide			Moderately wide			Slightly narrow			Narrow			Very narrow	
Thickness of finish,		Very thick				Thick or extremely thick			Moderately thick			Slightly thin			Thin			Very thin	
Plumpness of leg of lamb,		Very plump				Plump			Moderately plump			Slightly deficient			Deficient			Very deficient	
Composite grade,*																			

* "Composite grade" means the one grade representing the entire animal.

LENGTH OF BODY

1. Very short.
2. Short.
3. Moderately short.
4. Slightly long.
5. Long.
6. Very long.

PELT

1. Very light.
2. Light.
3. Moderately light.
4. Slightly heavy.
5. Heavy.
6. Very heavy.

____
(Signature of grader)

FIG. 197.—Slaughter lamb grading chart.

depth of chest, length of body, height at withers, circumference of middle, and over-all length from nose to dock. A wool sample was also sent to the laboratories at Beltsville, Md., and scouring data secured. Wool scores and weights were taken on all the ewes in the flocks yearly. The weights and sexes of all lambs born were recorded.

On the basis of the data secured, correction factors for type of birth (singles and twins) and for sex were developed, those for the Southdowns being 5 lb. for females and 6.5 lb. for twins and for the Shropshires 4 lb. for females and 8.5 lb. for twins. At 140 days the weights of all lambs were standardized by use of these factors.

Five Shropshire and eight Southdown rams that were used in the two flocks show a considerable range as measured by their offspring, as indicated in Table 59.

These data on the Southdown and Shropshire flocks at the Massachusetts State College accumulated during the past 7 years are now in process of analysis and, it is expected, will be published as a bulletin in the near future.

At this time, it would seem that the following data would provide sufficient material for "record-of-performance" and selection procedures in the Down breeds of sheep.

1. Breeding and lambing dates.
2. Birth weights—sex—type of birth (single, twins, etc.).
3. Lamb weights at 30 days (to measure milking ability of ewes).
4. Lamb weights at 140 days.
5. Market grade and type of lambs at 140 days.
6. Fleece weights and grade when sheared and days of growth.

With these data we will perhaps have all the necessary tools for proving rams—for being able to say with some degree of certainty, this ram is a good one, his get are better than their dams in amount and quality of carcass and wool. He is so good in fact that we ought to do some inbreeding with him in order to render our flock more homozygous for his demonstrated superior genes. Or that ram is no good—his get are worse than their dams, the flock is retrogressing. We not only ought to stop using him as a sire but we ought immediately, and while it is still easy to do so, rid our flock of his bad genes by culling all his offspring.

The Western Sheep Breeding Laboratory was established at Dubois, Idaho, in 1937 with Dr. J. E. Nordby as director. It is utilizing the facilities developed by the Bureau of Animal Industry Sheep Experiment Station, which was organized at Dubois in 1917, and in addition the experiment stations of the 11 Western states and Texas are cooperating.

The main objective of the program is the improvement of sheep through breeding. The improvement is measured by the application of utility standards

as they concern commercial production under ranching conditions. Production is measured on the basis of wool yield, and in pounds of lamb of the desirable type and finish. Obviously, the staple length and the quality and uniformity of fibers, as well as the shrinkage, are important factors that are studied with the yield of wool. All useful type characteristics that influence lamb production, ranch adaptability, and general serviceability are closely integrated in the improvement program. Under ranching conditions at relatively high altitudes, where winter storms are frequently severe, the objectives in sheep improvement must also include a consideration of those characteristics in a fleece that protect the sheep against weather extremes. The fleece must be relatively long and "lofty" as well as dense and must hold together along the topline and cover well the underline.[1]

Attention in selection is being given to both meat and wool production but with meat qualities emphasized somewhat more than those relating to wool.

Besides we are interested in the mature form of mutton sheep on the basis of its value for producing the right kind of market and feeder lambs, and replacement ewes. While obviously the mature size, form, and fleshing quality of a sheep are important, the ranchman is perhaps fully as concerned with weight, form, and fleshing qualities at the time of weaning the lamb, because it is at this time that weight and form, but principally fleshing, will determine if the lamb is a market lamb or a feeder lamb. The milking quality in ewes is observed just after lambing, and this is further checked in their ability to produce vigorous and fleshy lambs. In the selection program, therefore, much emphasis is placed upon the finish in lambs at the time of weaning. Due consideration is given to twins in this connection. Stud ram prospects are scored carefully for market qualities at weaning, because a ram lamb that has the acceptable growth, ruggedness, form and finish at weaning time is probably more apt to be a potential sire of lambs of the same kind, than is a more slowly maturing ram that does not develop these qualities before he is more mature. Vigor is an essential quality in the selection of ranch sheep. Some ewes, and rams also, "wear" uniformly well under heavy service until they are seven or even eight years of age. Others begin to decline early in life and are on the "cull" list at five or before.[1]

Selection is being practiced against too heavy face covering that might lead to "wool blindness" and also against heavy skin folds.

The breeds being used are the Rambouillet, Columbia, Targhee, and Corriedale. Some 34 inbred lines are being formed with all rams progeny-tested before being used in an inbred line. The rate of inbreeding varies in the different lines and is based upon individual merit and performance in each line. It is expected that some of the inbred lines will excel in some respects, others in other respects, and, when the lines

[1] From mimeographed statement on the Western Sheep Breeding Laboratory and the U.S. Sheep Experiment Station by Julius E. Nordby.

have become relatively pure, the attempt will be made to combine as many of the desirable qualities as possible in one line by judicious crosses of the inbred lines.

Selection Indexes in Swine.—In selecting breeding animals in swine, we face problems similar to those found in all other classes of farm mammals, we know that the same natural laws of inheritance are operative, so that we expect to have to use a similar general type of procedure with its details modified to fit this particular class of livestock. In brief, we know that hereditary differences in fertility, nursing ability, rate and efficiency of growth, and quality of the finished carcass as well as differences in disease resistance, longevity, disposition, etc., exist

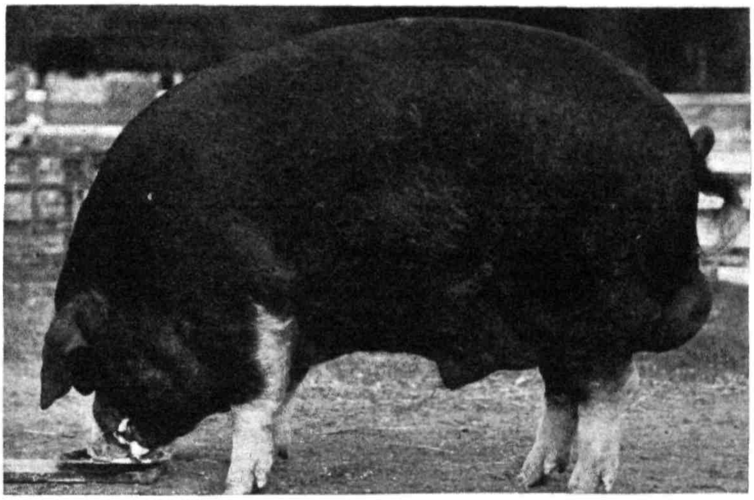

FIG. 198.—Poland-China boar The Hub, grand champion boar, Iowa State Farm, 1941. Owned by William Carver's Sons, Lamoille, Ill.

among individuals, families, and perhaps breeds of swine, and that our task is to develop practicable methods for measuring these differences so that we can increase our stock of good genes and rid it of poor ones.

Numerous investigations have revealed wide differences in rate and efficiency of gains in swine and since the main objective in growing swine is that of producing as much high-quality pork per sow with as high a feed-conversion efficiency as possible, this item should receive the main emphasis. In one investigation involving several litters of pigs, daily gains per pig among the litters ranged from 0.56 to 1.41 lb. per day, and the feed consumed per 100 lb. of gain ranged from 360 to 504 lb. One litter in other words was exactly 40 per cent more efficient in converting feed into flesh than was another of the same breed under exactly similar conditions. Translated into cash, this means that for every

$100 that a feeder with the low-efficiency pigs made (of course, he might not have made any money with hogs of this sort) the man with the high efficiency animals would make $140. The efficiency quotients of our animals vary over a rather wide range just as do the intelligence quotients (I.Q.) of our human population. Many of these differences (as measured) are probably environmentally caused, but, if even half of the difference is caused by heredity (the combinations of genes), it is well worth trying to improve by devising procedures to record the necessary data to divulge the facts, because, when we have the facts, we know how we can increase the percentage of good genes in a herd at the expense of poor genes.

Here, as elsewhere, what we need is an index of breeding value especially for boars because they leave so many more offspring than sows. This index could be formed from the progeny performance alone but ideally should consist of a contrast between a group of sows and their offspring. If we can hold the environmental influences between the sows and their offspring relatively constant or devise correction factors for differences due to environment, then the gain or loss in any desired quality can justly be attributed to the influence of the boar's heredity.

We could start with any crop of pigs, some of the females of which are going to be saved as breeding sows. We could record the birth weights of these sow pigs, their weights at 56 days, and their daily rate of gain under standard conditions of feeding and handling up to six months of age, and we could rate them on the basis of their suitability as to market type at this time on a scale ranging from 1 (top) to 10 (bottom). When they in turn had a litter of pigs, we could get the same records on their pigs. We might then have something of this sort.

	Average birth weight	Average 56-day weight	Average daily gain	Average grade score
6 sows	2.4	32	1.1	4.3
40 pigs	2.6	38	1.3	3.8
Boar's index	2.8	44	1.5	3.3

This is evidently a very good boar, for the index shows that he is siring larger, faster growing hogs of a better general-market grade than were the sows to which he was bred. Since the sows were not pushed as pigs to make the most rapid gains possible and some at least of their offspring were, we would need a correction factor to smooth out this difference. Likewise, the weight per pig at birth is influenced by the number in the litter, the age of the sow, etc., so that these features might need correction factors.

Such data would also reveal marked differences between individual sows. Some of them produce larger pigs that grow more rapidly into more desirable grades of market hogs. In making selections of gilts to be retained for brood sows, these considerations should weigh heavily. Figure 199 gives a sample of conditions existing in the Massachusetts State College herd of Chester White swine in the summer of 1941.

Bay State 34 of 1938

	Born	Raised	Weight of pigs	
			Birth	6 weeks
1939	10	10	2.8	30
1940	12	10	2.7	17.3
1940	12	10	2.8	26.5
1941	11	9	2.5	27.4
Average.	11.2	9.7	2.7	25.3

Silver Prince
311 pigs
Average birth weight 2.71
Average 6-weeks weight 23.9

Bay State 7 of 1936

	Born	Raised	Weight of pigs	
			Birth	6 weeks
37	7	6	2.5	25.3
38	9	9	2.4	26.6
38	12	10	2.8	24
Average.	9.3	8.3	2.57	25.3

Bay State 2 of 1939

	Born	Raised	Weight of pigs	
			Birth	6 weeks
1940	15	10	2.3	17.4
1940	15	6	2.3	20.2
1941	12	7	2.4	21.1
Average.	13	7.7	2.3	19.6

Silver Prince (See Above)

Bay State 4 of 1936

	Born	Raised	Weight of pigs	
			Birth	6 weeks
1937	9	9	2.6	21.2
1938	8	5	2.1	22.4
1938	10	6	2.7	20.0
1939	14	10	2.0	21.2
Average.	10.2	7.5	2.3	21.2

Fig. 199.—Performance data of two Massachusetts State College sows.

The data on only two sows are shown here. Both of these sows were of acceptable Chester White type and were by the same boar and had been bred to the same boar.

Bay State 2 is a somewhat better type sow than is Bay State 34, having a stronger, better arched back, a smoother shoulder, and a slightly stronger pastern. When these sows and their litters were being inspected with a view to picking out some sow pigs to be saved for breeding purposes. Bay State 2 was in much better flesh also. She had had and raised a smaller litter than Bay State 34, who had milked down into rather

thin condition. There was little to choose in external appearance between the best sow pigs of these two litters except the greater size of Bay State 34's pigs, but there was considerable difference in uniformity, very much in favor of Bay State 34's pigs, which were an exceptionally uniform group.

The data shown in Fig. 199 are by no means as complete as they might be, as we should like to have the average weights of these pigs at six months of age, their efficiency quotient in converting feed into pork (100 lb. gain divided by amount of feed required for 100 lb. gain), the dressing percentage of those which had been slaughtered, as well as their carcass grades. We would like also to have all this information on both granddams of these two sows, as well as additional information on their sire Silver Prince and the two grandsires. Nevertheless, it was not difficult to reach a decision to keep two sow pigs from Bay State 34 and not to keep any from Bay State 2, in other words, to let the Bay State 2 line die out because the line is apparently lacking in nursing ability and the ability to raise a goodly proportion of the pigs born at a rapid rate of growth.

Both the Hampshire Swine Registry and the United Duroc Record Association have set up systems for recording performance on the part of sows, the former breed calling theirs a Registry of Merit (R.M.) and the latter a Production Registry (P.R.). The rules governing these registries are very similar in both breeds and include:

1. Availability only to registered purebreds in the breed, with no outstanding faults (D).

2. Freedom from swirls, hernia, cryptorchid pigs, white feet (D), and at least 10 good teats and no inverted teats (D).

3. Litters ear-notched at farrowing, witnesses or affidavit (H), farrowing reports within 3 days (D).

4. Weaning weights of litters taken at 52 to 60 days with witnesses and calculated to 56 days.

5. To qualify a sow:

Hampshire	Duroc
2 litters of 8 pigs	2 litters—total 16 pigs
320 litter weight and all pigs over 25 lb.	Total 2 litters 640 lb.
Sows must pass type inspection	

6. Gilts under fifteen months—litter weight corrected by factor 1.15.

7. Sows—gold star on R.M. or P.R. certificate for each qualifying litter.

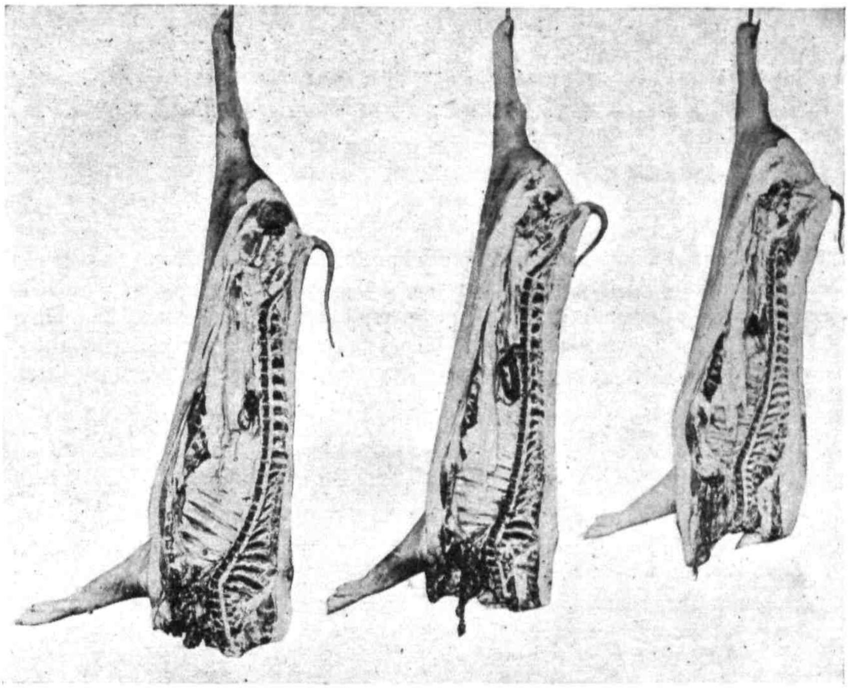

FIG. 200.—Dressed carcasses of large-, intermediate-, and small-type hogs, slaughtered at approximately 225 lb. in weight. (*From O. G. Hankins, A Study of Carcass Characteristics in Relation to Type of Hog, Proc. Amer. Soc. Anim. Prod.*, 1940.)

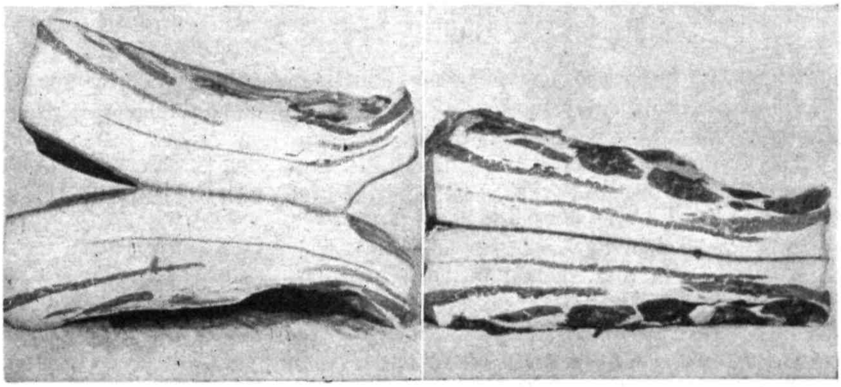

FIG. 201.—A contrast in the proportions of fat and lean in bacon, associated with a difference in breeding. The final feed lot weight of each hog was approximately 225 lb. (*Courtesy of Bur. Anim. Indus.*)

litters. Then, in turn, test their offspring. In this way, you will soon know the truth about your herd. Picking a few of the best to test each year may perhaps make your herd look better for the time being, but it will leave you as ignorant of real facts at the end of 10 years' work as you were at the beginning.

This is an excellent start and is meeting with strong backing on the part of Swine breeders with nearly 1,000 spring litters entered in 1941. It is a cooperative arrangement between the individual breeder and his breed association. This kind of cooperation is bound to succeed if it is founded on a firm scientific basis and will have financial advantages to those who participate. Some may think this sort of thing is going to take all the fun out of breeding, that if we are not gambling a bit it

Sire—weight 820 lb. All his pigs average 2.73 lb. at birth. All his pigs average 43 lb. at 8 weeks.	Grandsire—47 P.R. daughters. 61 P.R. sons, weight 860 lb. Average weight all pigs, birth, 2.76 lb.—8 weeks 44 lb.
	Granddam—18 P.R. daughters. 12 P.R. sons, weight 700 lb. 16 teats. Average weight all pigs birth, 2.61 lb.—8 weeks, 41 lb. Average litter size 11, raised 10.
Dam—weight 630 lb. 14 teats. Average litter size 13 pigs, 11 raised. Average weight of pigs at birth 2.81. Average weight of pigs at 8 weeks 41 lb.	Grandsire—6 P.R. daughters. 21 P.R. sons, weight 840 lb. Average weight all pigs, birth, 2.47 lb.—8 weeks, 40 lb.
	Granddam—41 P.R. daughters. 16 P.R. sons. Weight, 640 lb., 14 teats. Average weight all pigs, birth, 2.52 lb.—8 weeks 41 lb. Average litter size 11, raised 10.

FIG. 203.—Pedigree of a boar of tomorrow.

can't be any fun. Well, don't worry—you'll still be doing enough gambling to make it fun only perhaps not enough to completely break you.

It will be nice when we can write the pedigree of a young boar as indicated in Fig. 203.

The above pedigree has some real meaning to the average breeder. It gives him besides names—which are important—some records of commercially valuable characteristics. It gives the weights of the animals and the number of teats on the female. Since the parents and grandparents are all R.M. or P.R., they must have been of good acceptable type. It gives a measure of prolificacy in litter size, of vigor of pigs in birth weights, of growthiness in weights at 56 days, which also measures milking qualities of the sow and of maternal characteristics of sows in the number or percentage of pigs raised. Such pedigrees will be common in "Hog Breeding of Tomorrow." This R.M. or P.R. system, under proper management and safeguards by their breed association, will be a great help to a group of breeders. It will provide sound facts on which

they as individual breeders as well as the breed as a whole can move forward confidently.

This is really a constructive start on a difficult problem. Some may be inclined to criticize it for not getting enough data, but other records can be added as experience dictates the necessity. It is an established fact that the bigger pigs at birth grow faster and reach marketable weights earlier. It has also been established that there is a correlation between rapidity and efficiency of growth. Eventually, efficiency of feed conversion can perhaps be included in the testing and also an evaluation of carcasses from a cutout standpoint. The writer thinks the Hampshire Registry Association and the United Duroc Record Association are to be congratulated for keeping the production requirements relatively simple in the beginning. The real evil to be guarded against is that mentioned earlier regarding "selective" testing. Testing a few of the best offspring of breeding animals yields nothing of enduring value. Eventually, we may be able to prove boars just as we now prove dairy bulls or racehorses. If the sows to which a boar is mated came from litters of 10 that weighed 2.2 lb. at birth and 34 lb. at 8 weeks, whereas their litters by this boar averaged 14 pigs weighing 2.6 lb. at birth and 41 lb. at 8 weeks, we can get a direct measure of this boar's transmitting abilities in these regards, and we can index the boar for these various characteristics, but we must, of course, realize that only 50 per cent or less of the variation in our animals is due to heredity.

This is the first and most important business of a breed association, *viz.*, to set up a practical system that breeders will adopt and use. This will furnish the much-needed records without which really intelligent breeding is impossible. By this means the whole breed can be analyzed. Some families and strains will be found to be better than others in one or another respect, and vice versa. The really poor strains in the breed should be rapidly weeded out. These records, in plain words, will really allow us to know our breeds their good and weak points, their good and weak families. This is analysis.

Then the fun can really start, for after analysis logically comes synthesis. Complete breed analysis will make breeding easier in some respects but much more difficult in others. Some families will no doubt be found to be superior in one or more respects; some in another. The job of the breeder then will consist of introducing enough foreign blood into his strain to strengthen some of its weak points, but it is a rather delicate balance that he is working with, and the scales can all too easily be tipped too far. Selection itself will be much easier on the basis of more complete records and data. As seen from the illustrated pedigree, the choice of boars should be much easier when pedigrees can be written more fully in terms of records.

The other phase of selection is, of course, the selection of the females within one's own herd. When a series of a few proved sires have been used, however, it will be possible for the breeder to analyze and chart his own herd in such a way that more intelligent selection of female lines can be made.

With the P.R. or R.M. data available, some very interesting comparisons might be available. We might find that the average litter size in one family was 11 pigs with 10 raised, whereas in another family the average litter size was 8 with 6 raised. Likewise, the first family's offspring might have averaged a birth weight of 2.7 lb. per pig with a 56 days' weight of 40 lb., whereas the other family's pigs averaged 2.2 lb. per pig with a 56-day weight of 32 lb. With the data available in this form, a breeder is in a position to practice really intelligent selection in the female lines in his own herd. If he does this and can get pertinent data on the boars that he buys, he should be able to make steady progress in his breeding operations.

The formula for a better breed, then, is this coöperative effort between the breed association and the individual breeder. The association provides the organized leadership, furnishes the breed ideals and a practical mechanism for getting accurate records, on which alone we are able to base a fair estimate of the genetic determiners of characteristics which our animals possess and on which their breeding worth entirely depends.

The individual breeder tests fairly the animals in his herd and on the basis of these proved data selects his breeding females and his boars. The breeder still retains his "rugged individualism," for he alone decides which gilts to save, what boars to use, and whether to linebreed, inbreed, or outcross. If the decision is to linebreed to some particularly desirable animal, the breeder must decide how close to go. Shall he breed sire to daughters or play a little safer and mate him to granddaughters? Even when we get complete records on our breeding animals, there will still be the exciting and important job of planning matings. The science of breeding and obtaining records are merely aids and guides to the art of breeding.

The qualities most desired in present-day hogs can be very well-illustrated by the following Platform for Hampshire Type Development as set up by the Type Committee of the Hampshire Swine Registry and revised to date at the third annual type conference held at Purdue University in June, 1941.

A. Productiveness

Improvement of market pork production is the only function of the purebred hog business and profit to the pork producer is the first consideration.

1. A superior prolificacy is one of the most valuable of Hampshire characteristics and is to be jealously guarded and maintained as one of the prime requisites of the breed.

2. Ruggedness, feed utilization capacity, the ability to produce plenty of milk to support big healthy litters and highly developed mother instinct to get those bigger farrowed litters into the feedlot—must be insured.

3. Adequate length is essential and at least six good roomy teats, properly spaced, shall be insisted upon on each side of the udder of sows and gilts and of rudimentary teats also on boars. On mature sows there shall be definite indication of good udder development.

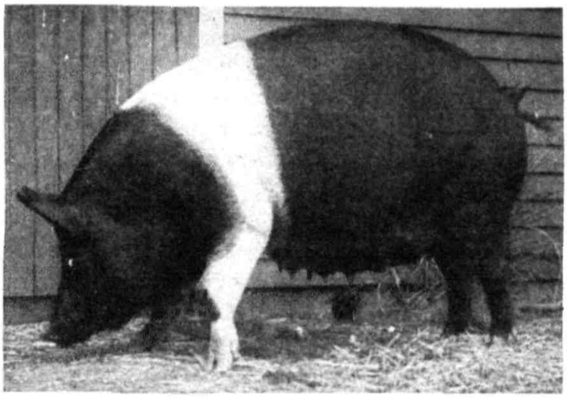

FIG. 204.—Hampshire sow, Main Line Beauty 2nd. The first Registry of Merit sow of any breed.

4. Superior Hampshire vigor, hardiness and foraging ability are to be maintained as important assets in profitable production.

B. Feeding Quality

The Hampshire objective is a middle-of-the-road hog which can be finished at around 200–225 pounds at 6 months of age or which can be profitably carried on to heavier weights when market conditions warrant.

1. An extra meaty, full-fleshed, deep-sided body, set on strong legs of medium length, is indicative of both feeding ability and early maturity.

2. Strong legs over short strong pasterns are to be squarely set on the corners with ample width between both the fore legs and the hind legs.

3. Width between the eyes, and a broad, full face and snout are to be sought; small, thin fox ears and thin rat tails avoided.

4. Rugged quality without fineness is to be carefully maintained.

C. Market Qualifications

Since the primal cuts of ham, bacon, loin and shoulder, constituting but 45% of the live weight, total 80–85% of the carcass value, the points of individuality corresponding to these cuts are of great importance.

1. Depth and fullness of ham, extending down to within two inches of the hock, is to be very especially emphasized.

2. The tail head shall be set high to avoid steepness of rump and to increase the depth of the ham.

3. Depth of straight side and a fullness and thick fleshing of flank to develop a straight underline are to be strongly emphasized. Increasing depth of side must be accompanied by increased length to insure proportion of bacon cuts and a desired increase in length of loin.

4. A uniformity of width from end to end is to be insisted upon, insuring fullness of loin and fullness behind the shoulder.

5. A uniform gradual arch of back from end to end, but of moderate height, is to be preferred rather than an excessively highly arched back.

6. A meaty shoulder of reasonable spread across the top is desirable but it must be in line with the rest of the body, with no depression behind shoulders, either on top or on the sides.

D. Meat Type

Since excess lard production continues as the most serious problem of the hog business, the distinctive Hampshire meat type is to be maintained with no increase in lardiness.

1. The fleshing shall be unmistakably firm and solid, even when in high market condition.

2. A wasty middle, wrinkled flabby belly, heavy jowl and in boars an excessive sheath are to be avoided.

3. Full medium width of back is desired rather than extreme width and with a strong gradual arching of the ribs above a straight deep side rather than an excessively broad, flat spring of rib.

The above general ideals could probably be applied to swine of any breed together with the specific qualities as expressed in the various breed standards of perfection. Provided with a phenotypic ideal and a system of measuring, recording, and printing pertinent data on production accomplishments of sows in terms of their fertility, nursing, and motherly qualities together with accomplishments of their offspring in terms of ability to grow rapidly and efficiently into desirable animals from a meat-carcass standpoint and the possibility of using these data for indexing boars, the breeding of swine is rapidly being put onto a sound genetic basis. As in all other classes of livestock, the first task is that of analysis, of discovering through record keeping the best individuals and strains within the various breeds. When this has been accomplished, there will remain the further task of fitting together the discovered best of several strains as to different desirable qualities and the rendering of this germ plasm relatively homozygous through judicious amounts of inbreeding.

A word of caution should be injected here, and as an example we will use hams in hogs, although the general idea is probably applicable to many other type qualities. Workers in the Bureau of Animal Industry

have found that "there is a *negative* correlation between slope of rump and ham yield ($r = -.34$), also between plumpness of ham and ham yield ($r = -.31$); *i.e.*, the leveler the rump and the plumper the ham, the smaller the *per cent* of ham in the carcass. This doesn't mean that the ham from a hog with level rump and plump ham is less desirable, but it does mean that any advantage is *not* due to a *higher yield* of ham."

In Iowa the extension service is sponsoring a swine-herd-improvement plan. A record is kept by breeders of the number of pigs farrowed per litter, number raised to eight weeks of age, and the weight of the litter at 56 days. In this way the individual sow's worth regarding fertility and ability to suckle pigs is measured. Later, representative pigs from each litter are to be judged from the standpoint of suitability on the hoof, and then slaughtered to obtain dressing percentages and cutout values. The standards are seven pigs per litter for gilts, eight for sows; litter weights at 56 days, 225 lb. for gilts and 250 lb. for sows.

The matter of testing sows has probably been carried further in Minnesota than in any other state up to the present. Prof. H. G. Zavoral, Extension Animal Husbandman at the University of Minnesota, has made the following very interesting report on this work.

The object of sow testing is to develop strains of hogs that will give the best returns over feed costs per 100 pounds of gain. It is a method of finding and selecting the most profitable breeding stock. The continued testing of sows is an important factor in developing strains that will have an inherited rate of rapid and efficient growth.

A record of performance test for sows was begun in Minnesota in 1929. Breeders of purebred hogs were invited to send four pigs, two barrows and two gilts, from one of their best litters to the experiment station at weaning time or when 56 days of age. Since prolificacy is an important factor in hog production cooperators were asked not to send pigs from litters unless there were at least seven pigs weaned from a gilt and eight pigs from an older sow.

The four representatives from the same litters were fed a standard ration at the experiment station until they reached 225-pound weights. At this weight three of the four pigs were slaughtered and a careful study made of the carcasses to determine how closely they met market demands. In addition to the records of the rate and cost of gains obtained during the feeding period, the breeder reported the weight of each pig of the litter at 56 days of age. In this way a measure of the uniformity of the litter was established.

From records obtained over a period of three years, differences in feed costs, in gains, and in carcass values of purebred hogs were studied. It was found that there was a difference in daily gains of slightly more than one-third of a pound per pig and a spread of 72 pounds in total feed required to make 100 pounds gain. There was also a variation in average dressing percentages of 4½ per cent, and a difference of 86 cents in the average value of carcasses, calculated upon 100 pounds of live weight of a finished hog. The average daily gain per pig ranged from 1.10

to 1.64 pounds and feed totals for 100 pounds of gain varied from 345 to 419 pounds, and a difference of $2.00 in the value of a 225-pound hog carcass showed up.

These facts clearly pointed out that there was a difference in the strains of hogs regarding feed costs and carcass values. Thinking along this line paved the way for a method in selecting breeding stock. It was agreed that since hogs are graded on the hoof and not on the hook, the producer is looking for the heaviest hogs in the shortest time on the least amount of feed. Just how much of a hog's ability to make rapid, economical gains may be attributed to inheritance is hard to answer. But because dairymen have made progress by continually keeping breeding stock from the highest producing dams, there appeared to be no reason why hog producers could not do the same thing. The nearest approach thus far devised toward that end is what is known as sow testing.[1]

A sow-testing project was organized in Minnesota in 1934 with 63 farmers enrolled, but only 25 per cent of them marked and weighed the pigs at weaning, and still fewer weighed them at six months. In Fillmore and Houston counties in 1937, 45 farmers hired a sow tester who made the weighings, kept the records, etc. for a period of 2 years. The work was carried on in 1939 without a sow tester and has stimulated many swine breeders to do more careful selecting in their herds. The plan is based largely on weights, and those carrying it on realize that it should also include measures of economy of gain and quality of finished carcass.

Results from this effort after three years' experience showed that some litters weighed much more than others at weaning time, even when difference in size of litters was allowed for. The heaviest litters at weaning time continued to be the heaviest throughout the growing period. Sows were culled on the basis of weight per litter at weaning and gilts for breeding were selected from these heaviest litters. Cooperators reported marketing their hogs in 6 months instead of 7 and 8 as formerly. One man reported 210-pound pigs in 5 months. He attributed the increased weights more to the selection of breeding stock than he did to better feeding. The producers that followed sow testing were sold on the results. The trouble lay in that only an insignificant number would cooperate. They just would not do the necessary work themselves. This, we learn, is also true in cow testing. If a regular tester does not come around to do the detailed work, farmers will not do it.

Sow testing will continue to prove that there is a difference in hogs. Our records show that some sows will produce twins and triplets weighing 20 to 30 pounds apiece at weaning time and only 150 pounds at 6 months of age. On the same farms other sows will save 10 to 12 pigs at weaning time weighing 50 pounds apiece and over 200 pounds at 6 months of age. Before purchasing boars for future use, swine growers will want to know more and more about the record of performance of their ancestors.[1]

[1] ZAVORAL, H. G., Sow Testing in Minnesota, *U.S. Dept. Agr., The Extension Animal Husbandman*, March, 1940.

A regional swine-breeding laboratory was established at Ames, Iowa, in 1937, under the authority of the Bankhead-Jones Act of 1935. According to the director, Dr. W. A. Craft, "The primary objectives of the project are to test adequately the application of certain breeding methods for general improvement of swine and to develop measures of such characters as productiveness of sows, rate and economy of gain, general vigor, and carcass merit which may be used effectively to supplement the methods of selection now being generally followed." In other words, this is a definitely organized project to explore the possibilities of progeny testing based on records of performance as an aid to type and pedigree in the selection of swine. Dr. Craft says further,

> It is common knowledge that the crossing of established breeds, since the breeds were formed, usually results in an increased rate of growth and general vigor. However, crossbreeding does not solve the need for further improvement of the breeds since the maintenance of purebred stock is required even for crossbreeding. We believe that further improvement of the breeds should enhance their value as pedigree stock and for crossbreeding purposes also.

The present ideal in swine is for a thick, meaty type with shapely cuts throughout and a maximum amount of lean meat and a minimum of firm fat at handy slaughter weights. The performance of hogs at the Canadian pig-testing stations has shown that this type of animal (suitable for production of Wiltshire sides for the British market) can be as efficient in both the breeding pen and the feed lot as any yet known.

Cooperative experimental work under the general supervision of the Regional Research Laboratory is under way at the Iowa, Minnesota, Missouri, Nebraska, Oklahoma, Illinois, and Indiana experiment stations as well as at the National Agricultural Research Center at Beltsville, Md. The pigs are scored when they reach a 225-lb. weight on the basis of the chart shown in Fig. 205.

Individual scores, on a scale ranging from 1 to 9, are kept on the 225-lb. hogs for the separate items of head, shoulder, length of body, depth of body, shape of hams, length of legs, shape of rump, shape of back (side to side), and arch of back in the hope that they may be useful in studies of relationships between conformation of certain characters, rate of growth, and carcass merit, and at the same time make it possible to detect and record certain differences which may result between lines and perhaps between sires.

Similarly, measurements are being taken of the 225-pound hog as regards its straight-line length from base of ear to tail setting, depth of body from top of shoulder to arm pit (by means of calipers) and length of fore-leg (by means of a tape) in the hope "that these data may serve in appraising the value of certain scores for live pigs and aid in finally

CHART I

Scoring Chart for Pigs

Animal No.__________ Date__________

Breed__________

Score	9	8	7	6	5	4	3	2	1	Remarks
Vigor, health, and thriftiness	Superior +	Superior	Superior −	Strong +	Strong	Strong −	Weak −	Weak	Weak +	
Quality	Excellent +	Excellent	Excellent −	Good +	Good	Good −	Poor −	Poor	Poor +	
Length of body	Long +	Long	Long −	Medium +	Medium	Medium −	Short −	Short	Short +	
Details of conformation	Superior +	Superior	Superior −	Good +	Good	Good −	Inferior −	Inferior	Inferior +	
Animals as whole	Superior +	Superior	Superior −	Good +	Good	Good −	Inferior −	Inferior	Inferior +	
Grade	Choice +	Choice	Good +	Good	Medium +	Medium	Cull −	Cull	Cull +	

FIG. 205.—Scoring chart for pigs. (*Swine Regional Research Laboratory.*)

providing a quantitative description of an ideal hog at 225 pounds weight."

Systems of breeding including various degrees of inbreeding of 3 to 5 per cent per generation (four sires in a herd closed to outside blood), of 6 to 7 per cent per generation (two sires in a herd closed to outside blood), and of 11 to 12 per cent per generation (one sire in a herd closed to outside blood) as well as crossbreeding between two established bacon breeds are being utilized, and ordinary selection based on rate of growth to 180 days of age in a closed herd but with the inbreeding kept at a negligibly low level. When the inbred lines have become established, they will be used in single and double crosses within lines and for top crossing of boars on noninbred sows. The Poland-China, Duroc-Jersey, Hampshire, Chester White, Tamworth, and Danish Landrace breeds are being used in this experimental work.

Progress reports from the cooperating stations reveal many interesting facts about inheritance in swine for both commercial and noncommercial qualities. When the various projects have reached a greater degree of completion and, enough material for statistical analysis has become available, we can confidently expect that a great deal of extremely valuable information will be made available to swine breeders.

With breed associations, county and state-wide groups of producers, the Bureau of Animal Industry Regional Laboratory, and various state experiment stations all busying themselves with record-of-performance plans and instituting experimental procedures in studies of the effectiveness of the various systems of breeding, the prospect for improving our swine from the standpoint of their genetic make-up regarding their commercially desirable qualities seems very hopeful to say the least.

Summary.—In this chapter, we have reviewed some of the evidence which indicates so clearly that there exist wide hereditary differences in our meat animals for the efficient production of high-quality carcasses. The problem has seemed to boil itself down to that of formulating practicable methods for securing record-of-performance data for beef cattle, sheep, and swine which will accurately measure each male's genetic contribution to a herd or flock by allowing comparisons between the breeding females and their offspring in terms of the qualities sought. Each class of livestock has certain additional qualities or characters that must be selected for besides the main one of efficiently turning feed into flesh, *e.g.*, health, vigor, longevity, fertility, prolificacy, type, etc. The purebred breeder must also pay attention to breed trade-marks. Selection in meat animals will continue to use the old standards of individuality, because in these classes "type is production" to a very great degree. We will also continue to use pedigrees, and it begins to

look as though pedigrees can shortly be made much more meaningful by the inclusion of actual records of direct ancestors and collateral relatives. And to these two very useful selection indexes, we can perhaps shortly add the most useful tool of all in practicing selection, *viz.*, records of performance.

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[1] See also Appendix A.

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CHAPTER XXVI

RETROSPECT AND PROSPECT

We have now completed our discussion of the principles underlying the creation of better livestock. We tried to start at the beginning, to get some idea of the probable origin of life on the planet Earth something over 1 billion years ago. We concluded that something comparable to the gene must have appeared fairly early in this process. These entities, capable of certain reactions among themselves and with their immediate environment, the cytoplasm of the cells, and endowed with the power of exactly reproducing themselves, seem to have been proved without reasonable doubt to be the mechanism of inheritance in all living forms today.

From the point of view of logic, it seems probable that the genes have always performed this function. In the earliest stages, there perhaps was formed wave after wave of the simplest sort of living material that flourished for a short time and then quickly faded out of existence as living things without leaving offspring. At some stage, however, we must suppose that bits of this living material in some way became endowed with the property of reproducing themselves, so that as the old died, the new was born. Once started and with the occasional production of something a little different from the parent form we have the basis for an evolutionary process. At present a new and somewhat different living thing can arise only from other living things by means of the genes. They are today the fundamental mechanism of life, as evidenced through reproduction. It seems likely that they have always fulfilled this role.

We hurriedly traced the process of evolution until it finally gave rise to the larger farm animals and to man himself. We sketched the story of man's progenitors until modern man, *Homo sapiens*, appeared on the scene some 25,000 to 50,000 years ago. Then we saw man take one of his greatest forward strides some 8,000 to 12,000 years ago when he began to domesticate plants and animals, which better ensured his food supply.

We then sketched the progress that man has made through historic time in breeding, selecting, and perfecting his animals for specific purposes, and finally we find ourselves in the twentieth century with well-nigh perfect individual animals in all the classes of livestock but with the

average type and performance of our livestock well below an efficient and profitable level.

Our next task was that of learning some of the details of the workings of the intricate process of reproduction. In the lower forms of life, this process is relatively simple consisting merely of fission or division of the parent into two offspring. Next came budding, one or a few unspecialized cells having the power of creating a new individual. In time, specialized cells were developed for the reproductive function. Eventually, they came to be specialized in different ways, the union of two differentially specialized cells being necessary for the creation of a new life. Originally, these different cells were produced by the same organism, but they finally came to be produced by different members of the species, which gave rise to the sexes. At first, these male and female sex cells were passed to the exterior, where fertilization and growth took place. As organisms grew in complexity, so did the generative apparatus, so that in the higher forms of life we have, besides the glands producing the sex cells, a complicated mechanism of accessory glands and organs under the control of distantly located endocrine glands with fertilization and embryonic development taking place internally, the latter proceeding for many months and resulting eventually in the birth of a completely organized, though somewhat helpless and dependent, individual.

Research during the past 30 or 40 years has revealed many of the details of the workings of the generative organs in both male and female. Such knowledge provides a scientific basis for many practical measures in the management and feeding of breeding animals so that their reproductive powers may be utilized to the fullest extent by the breeder.

In the male, one of the very important practical developments has been that of artificial insemination, whereby the number of offspring left by really good breeding sires may be multiplied manyfold. The length of time semen may remain normal and the sperm retain their fertilizing power has already been extended to several days, with attempts in progress to extend this to months or even years. Experimental work is also in progress to find ways of feeding and managing good males so as to increase their output of semen and viable sperm and to extend the length of their breeding lives. Progress in these fields is being steadily reported.

In the female, systems of management to increase fertility and prolificacy are already known and in practice are taking the form of greater regularity of breeding over a longer span of years rather than an increase in the number of young born at any one time.

Artificial parthenogenesis has already been achieved in one mammal, the rabbit. Whether or not a scientific procedure for accomplishing this in the larger animals will ever be achieved remains to be seen.

What a boon it would be, for instance, in cattle if a particularly good cow could be made to reproduce parthenogenetically, provided, of course,

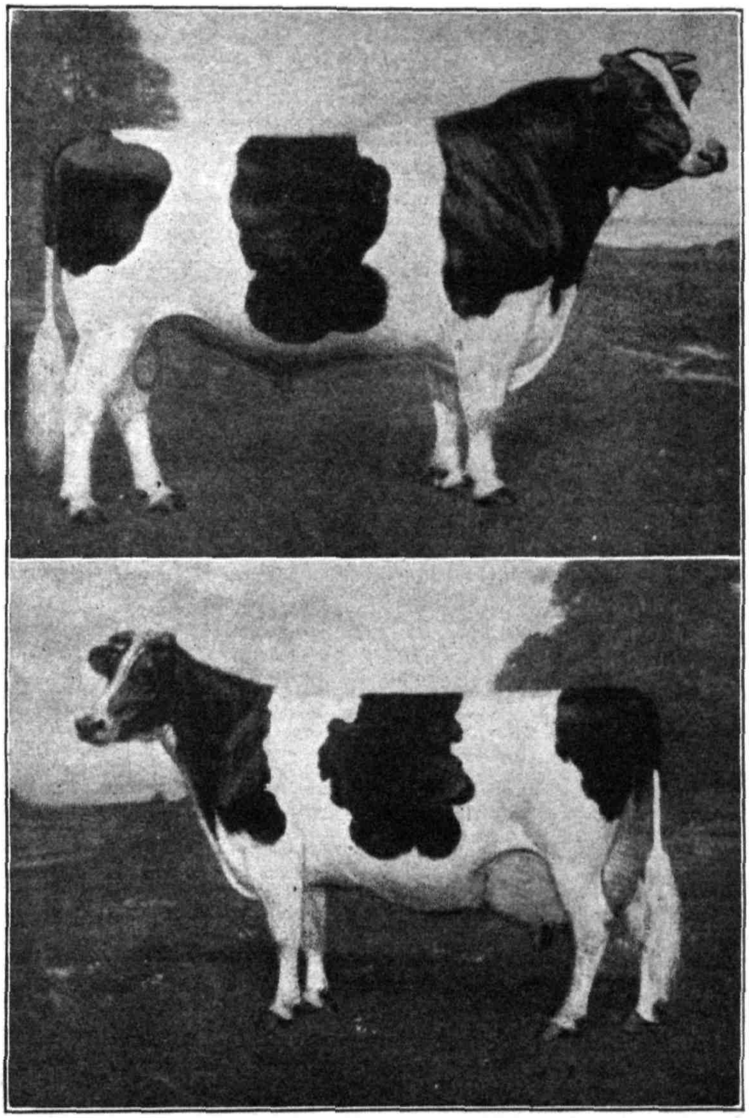

FIG. 206.—The "targets" at which Holstein breeders are shooting. Such models should prove invaluable in fixing type.

that she herself was relatively homozygous for the desirable genes, because we presumably would still have the sampling feature of inheritance as reduction took place in the formation of the mature egg.

Again, rabbit eggs have been secured, fertilized in a test tube, and successfully implanted in the uterus of another doe with the production in due course of livable embryos. Whether or not this technique can be perfected for a species like cattle is a problem for the future. If it can be, we can use our best cows for egg rather than for milk production, with the possible result that offspring from a given female can be increased manyfold, as has already been accomplished with males through the successful development of artificial insemination.

Developments to date in the field of the physiology of reproduction including the herd-health-association idea have already greatly increased

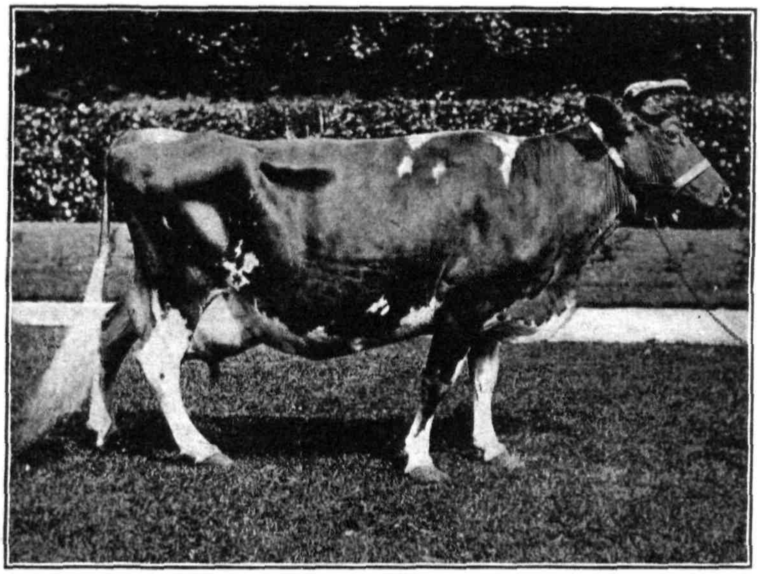

FIG. 207.—May Rose II, foundress of the May Rose family of Guernseys, noted for type as well as production. (*Courtesy of American Guernsey Cattle Club.*)

breeding efficiency. Sensible feeding and management along with the control of diseases of the genital tract have already put the bugbear of sterility on the defensive.

Tremendous strides have been made during the last 40 years in unraveling the heretofore puzzling and seemingly mysterious ways of hereditary transmission. Although the exact nature of genes is still unknown, experimental inquiry has yielded a wealth of information as to the varied nature of their reactions in determining the presence of specific characters. For reasons of expediency and cost, most of these discoveries have occurred in small, rapidly breeding species. Enough work has been done with the larger animals, however, to reveal the very great probability that the genes behave in these animals in exactly

the same manner as has been so abundantly proved to be the case in the smaller species. It is true that we do not have for any farm mammal even a beginning of a chromosome map, but this may be no great loss or deprivation, for, as far as the writer knows, the chromosome map of *Zea mays* has not served any utilitarian purpose in the recent remarkable progress in corn breeding.

An understanding of the basic principles involved in hereditary transmission gives the modern breeder a compass, with the north, south, east, and west quarters clearly marked, even though it is impossible yet completely to "box the compass."

Animal breeding is still an art, but it is coming to rest more and more securely on scientific foundations. We know that any animal arises from the union of a specific egg and a specific sperm; that the qualities of the new individual depend entirely on the genetic make-up of the egg and sperm, regardless of the phase of the moon, direction of the wind, etc. when fertilization takes place; that proper feeding and care of the pregnant female and the offspring after birth are necessary to bring its inherent capabilities to full fruition; that the sorts of germ cells which any animal can produce are determined by the genetic materials supplied it by its parents; that any animal passes on a sample half of its own inheritance, one member of each pair of chromosomes to each of its offspring; that age of itself has no influence on these chance combinations of hereditary units, *i.e.*, other things being equal, an animal will transmit similarly at one, two, ten, or twenty years of age.

And on the negative side we know that blood does not function in inheritance; that the kind of blood an animal has depends on the genetic content of the egg and sperm which gave rise to it, not vice versa; that acquired characters, telegony, maternal impressions, saturation, and other beliefs of a superstitious age can be consigned to the limbo of the never-was. In inheritance, genes and chromosomes are everything, all else nothing.

It is obvious, therefore, that we will have better livestock only when we have succeeded in so mating our animals that they automatically produce better germ cells, better in terms of being more homozygous for the genes and gene combinations making for more desirable qualities. Each planned mating which a purebred breeder makes actually covers two generations in the sense that it is designed not only to produce a good immediate offspring but one which will in turn be able to beget better offspring.

There are two major tasks awaiting the livestock industry as a whole. The first is the matter of analysis, or the finding out what we have genetically in our animals as they exist at present. We do not have and are not likely to discover any ways of creating new genes for improved

qualities in our stock. What our livestock will be like 10 or 100 years from now depends on two things: (1) what genes are present in animals now living and (2) our ability to discover the good genes and to increase their number at the expense of poorer genes.

We[1] have made remarkable progress in animal breeding in the United States since the days of the early settlers. Tough, wiry, streamlined cattle have been largely replaced by blocky, low-set high-quality bullocks;

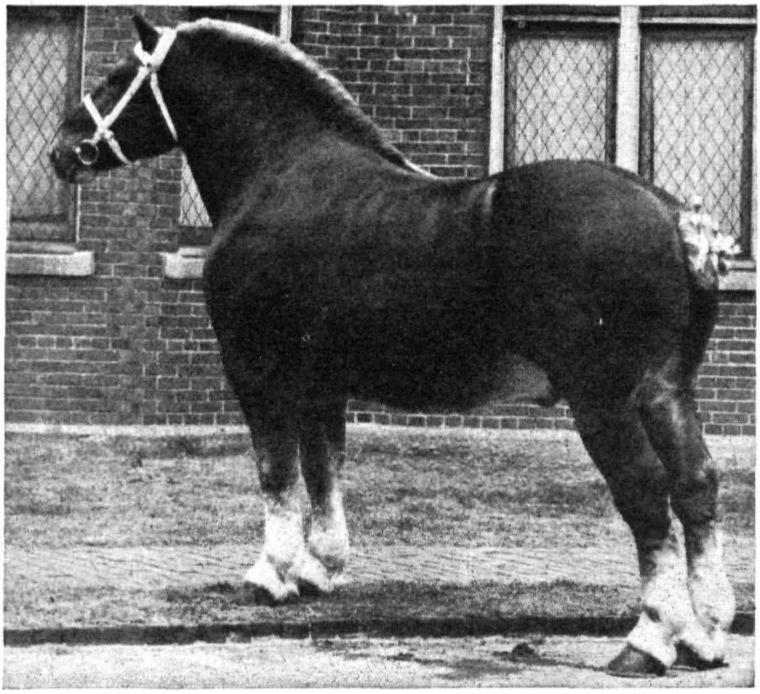

FIG. 208.—Belgian stallion Jay Farceur, grand champion International Livestock Exposition 1938, 1939, and 1940. Bred by J. W. Hillman, Grand Junction, Iowa, owned by H. C. Horneman, Danville, Ill.

our sheep have three or four times as much wool spread over a much more desirable carcass; our hogs are more prolific, more efficient, and speedier converters of grass and corn; our horses are heavier and better fitted in every way to relieve the physical burdens of food production; and our dairy cattle produce a greater quantity of a higher quality product than they did in Pilgrim days, in Civil War days, or even in World War

[1] Most of the material in the next six pages appeared originally as an article by the author entitled Our Breed Associations and was published in the March, 1939, issue of *Successful Farming*. It is reprinted here by permission of the Meredith Publishing Company, Des Moines, Iowa.

I days. Our methods may have been somewhat of a patchwork of guess, intuition, hocus-pocus, and ballyhoo, but what we had we used in typical, energetic American fashion. In the march of progress, our breed associations have had a more prominent part. That they have tended to be a bit conservative is probably a good thing.

A breed association is a group of men banded together for the pedigreeing, protection, and promotion of their particular breed. Most of these associations were organized after the year 1875, making them less than 75 years old at the present time. That they have accomplished great good no one acquainted with the facts would for one moment doubt. Like all things human, however, they have had and still have their failings. After 75 years of effort, and because they are recording societies, they should, it would seem, have records to which a breeder could turn for fairly accurate guidance in his job of breeding better livestock. They should now, in other words, be a real help to breeders, because they were organized for that purpose alone and long enough ago for results to have been achieved.

The greatest "lack" in breed associations today is the lack of records of performance. A pedigree that consists merely of names of ancestors without production performance of the ancestors and collaterals is of little value. If, however, the pedigree could be made complete in terms of records or characteristics, it would be an invaluable guide in the selective mating of animals. For example, if you have brown eyes and your parents, grandparents, great grandparents, brothers, sisters, cousins, aunts, and uncles all had brown eyes, then we would be reasonably safe in assuming that you would transmit only brown eyes to your children. In livestock, substitute for brown eyes such characteristics as hams, wool characters, loins, rounds, size of litters, efficiency of feed conversion or fattening, etc. Before we can hope for rapid progress in livestock breeding, a way must be found to get records of such performance characteristics on our breeding animals.

The U.S. Department of Agriculture, in cooperation with state colleges of agriculture, inaugurated surveys in 1936 seeking to discover superior breeding animals backed by adequate records. In beef and dual-purpose cattle, the 48 state colleges and experiment stations were able to furnish practically no data that might be useful in locating superior breeding stock. They were asked also to submit the names of breeders who might have such superior stock, and for the whole of the United States 11 stations furnished the names of 64 men—who were not surveyed because of the small likelihood of getting any data of real value. It was the same story in swine, although several stations were carrying on research projects dealing with the inheritance of characters of outstanding economic importance. "Because of the lack of results

out the desires of the breeders as expressed through the breed's executive committee or board of directors.

The value of Advanced Registry work, from a breed-improvement standpoint, has been negligible or worse. Thousands of excellent records have been made and many animals have been sold at long prices because of them, but we know now that an individual's performance and its progeny may be very dissimilar. Advanced Registry testing is like going into some city, finding the five prettiest girls in the town, and then inducing eligible young bachelors to believe that all the girls in said

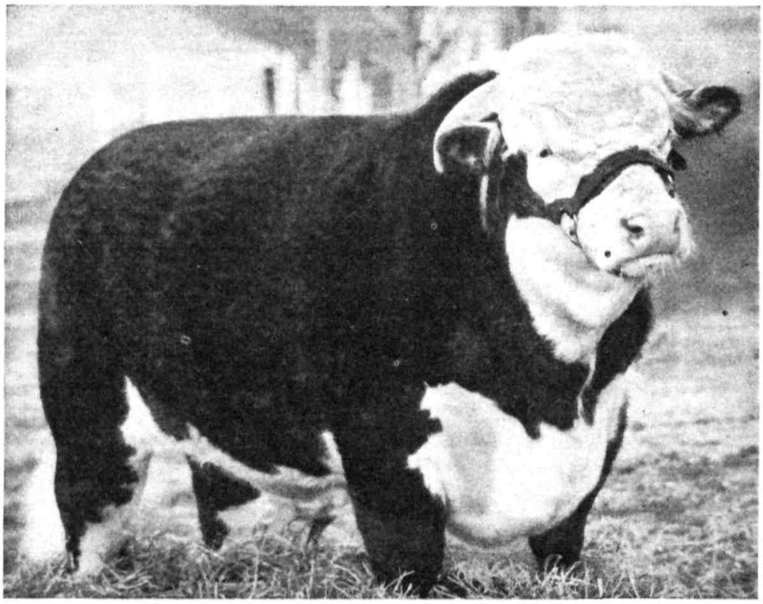

FIG. 210.—Hereford bull J. Royal Rupert 15th. Bred by Turner Ranch, Sulphur, Okla., owned by Hi-Point Farms, Romeo, Mich.

city are beautiful, and implying probably that they are also good cooks. No, selective testing is not worth the money it costs because it gives a distorted picture of the facts. The poorest bull that ever lived would probably have sired a few good daughters out of really good cows.

The herd test is a lot more satisfactory (records on all animals in a herd year after year), and such testing is now available in all the dairy breeds. Its use should be pushed much harder than is generally being done, and at the same time selective testing should be discouraged. Then, after the records are secured, they should be made readily available to breeders in a form that they can use in selecting breeding stock. The best way is on the basis of a comparison of the daughters' records with those of their dams. Some of the breeds are now doing this.

A fine system of recording D.H.I. Association records and getting valuable data quickly into the hands of the breeder has been set up by the Bureau of Dairy Industry, in cooperation with state colleges. If a bull is being used in a D.H.I.A. herd, we can write to our state-extension dairy specialist and get the breeding facts about the bull as soon as he has five daughters with records from dams with records, as these facts are published several times a year. The writer, nevertheless, believes that there is some danger in this plan because he does not believe that five daughter-dam comparisons are enough to prove a bull; in fact, he would demand twice this number. And, too, they must be an unselected, run-of-the-mine group.

From a breed-improvement standpoint the dairy-breed associations could well afford to discourage, and shortly give up entirely, selective testing, and try to induce their breeders to test all their cows every year. All the bulls could then be proved while they are still young and vigorous.

We are badly in need of something of this sort regarding our meat animals. There are probably two reasons that we don't have it: firstly, the fact that we are largely appraising visible qualities in our meat animals, loins, rounds, indications of quality, etc., rather than invisible things like milk production (therefore the need for factual data does not seem so great); and, secondly, the difficulties involved in getting factual data. Nevertheless, some beginnings are being made, as was indicated in Chap. XXV.

Our greatest need is records to prove breeding worth—records as to speed and economy of gains, quality of product, reproductive efficiency, amount and character of wool, longevity, resistance to disease, pulling and staying power, soundness, etc. The job is for each class of stock to set up its own standards and to find practical, economical methods of measuring its animal population against the standards. The purebred breeders, though their associations, should take the lead. It is a challenge that it would seem they cannot ignore.

The other major task awaiting the livestock industry, after that of getting records of performance, is that of fitting together these known ingredients in our animals into strains of animals which will surpass in performance anything that we have known in the past. This is the true art of breeding. In essence, it is merely applying the known principles of reproductive physiology and genetics through systems of breeding and selection in order to attain quickly and surely some preconceived ideal. Selection might be thought of as the anvil and systems of breeding as the hammer. Animals are tested in the fire of record keeping from which the best emerges in a somewhat purified state. Taking this tested material, the breeder with his hammer of breeding system shapes it according to his will against the anvil of selection.

The first problem which must be solved we can properly call *analysis.* Its method is that of recording essential data about the performance of our animals and its success depends largely on our ability to separate the environmental differences from those caused by inheritance, for only the latter are capable of being incorporated into the material passed along from parent to offspring. This second problem we can therefore call that of *synthesis,* the building up of strains of animals that are relatively homozygous for the qualities which make any given class of livestock desirable and profitable.

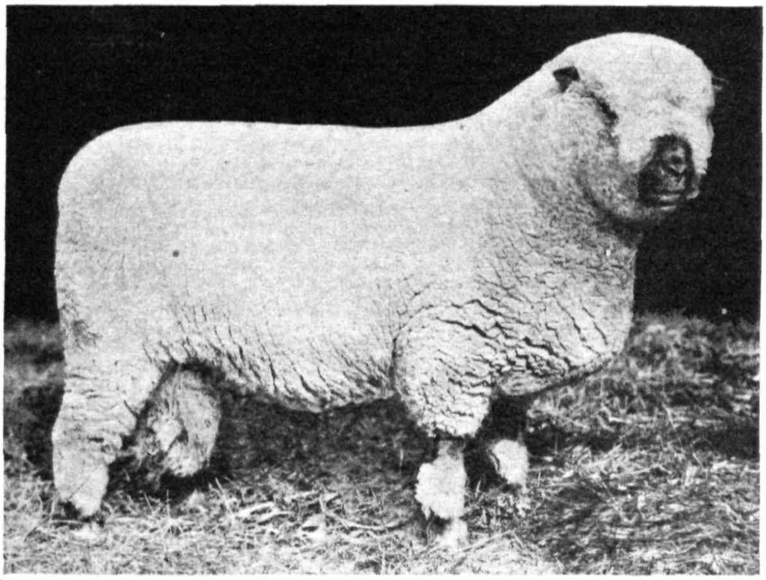

FIG. 211.—A model Shropshire ram, bred by George McKerrow and Sons Company, Pewaukee, Wis.

Up to the present, we have tried to practice this sort of synthesis on the information that we could get by studying individuality and pedigrees consisting merely of names, with perhaps a modicum of highly selected records to try to make pedigrees look as favorable as possible, extreme care being exercised to keep out any unfavorable data. It is, of course, human to try to put our best foot forward, and a breeder who told the whole truth about his animals would no doubt, temporarily at least, be at a great disadvantage compared with his fellow breeders who were telling only enticing half-truths. Our selection has been based, in other words, on phenotype and made-to-sell pedigrees.

The means of putting a firmer foundation under the whole of our livestock-breeding industry are now at hand. How should we proceed?

1. Study individuality with even greater care and diligence than we have in the past.

2. Get and print relevant breeding and performance data on our breeding animals. In other words, apply the progeny-performance test so that individuality can be more scientifically appraised and pedigrees written which will aid rather than hinder a breeder in arriving at a fair estimate of a young animal's probable performance and transmitting abilities.

The Holstein breed of dairy cattle has for a number of years been publishing indexes of bulls in the Red Book, which gives the summaries

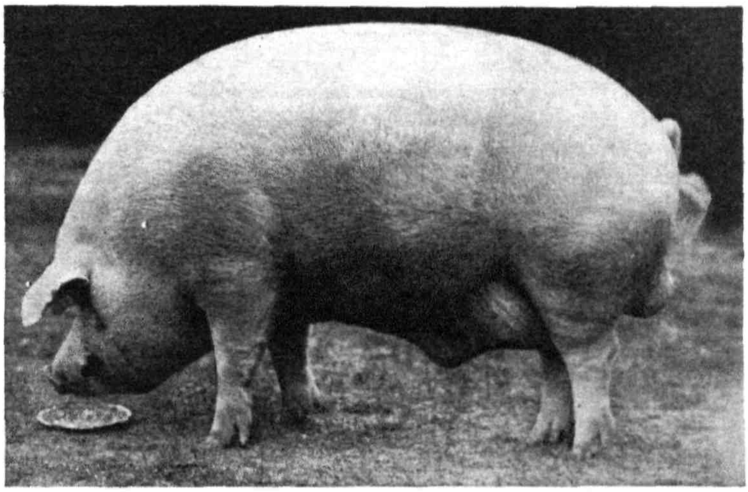

FIG. 212.—Chester White boar Modernistic, senior and grand champion boar at Illinois, Wisconsin, Indiana, and Iowa state fairs in 1941. Owned and shown by Frank E. Sherer of Joy, Ill.

of the herd test in this breed. Such records and indexes should prove to be of great value to Holstein breeders.

The Ayrshire breed is going to publish approved-sire lists for their breeders under the following stipulations.

Ayrshire bulls whose daughters have demonstrated their usefulness are to be officially recognized with the title of Approved Ayrshire Sires, following recent action of the directors of the Ayrshire Breeders' Association. To gain a place in this select group of the "bovine 400," a sire's daughters must meet each and every one of several stiff requirements that have been established by Leonard Tufts, well known breeder of Pinehurst, N.C., who for the past ten years has been privately conducting research on this subject.

Noteworthy feature of the Approved Ayrshire Sire plan is the attempt to secure a random sample of at least ten tested daughters, consecutive in the order of their birth. No sire is "approved" when there is evidence that the

daughters tested are a selected group. Due allowance is made for daughters that die before freshening, and those that are sold into herds that are not testing, but every daughter that freshens in the herd of a breeder who is testing is included in the average.

All records are first computed to a mature equivalent, 305-day lactation basis on two milkings daily by the use of standard factors of the Bureau of Dairying, U.S. Department of Agriculture. Ayrshire directors state that, in their opinion, a group of 305-day lactation records on twice-a-day milking is the most practicable yardstick by which to measure the daughters of a sire.

In addition to having a random sample of tested daughters, an Approved Ayrshire Sire's daughters must average at least 8500 pounds of milk or 340 pounds of fat, with an average test of not less than 3.9%. So as to not give approval to a sire whose daughters may be much lower than their dams, and at the same time meet the above standards of production, it is required than an Approved Ayrshire Sire must have an equal-parent index of at least 8500 pounds of milk or 340 pounds of butterfat, and a test of 3.9%

In an effort to approve only those bulls with a high percentage of daughters that are uniformly good, Mr. Tufts has added still another feature, requiring that at least 70% of all tested daughters must each make 8500 pounds of milk or 340 pounds of butterfat. Obviously, this will eliminate the sire with a few inordinately high record daughters that may contribute so much to the average of the entire group as to overlook several other decidedly low producers.

The analysis of the transmitting ability of bulls by this method is now a service furnished by the Ayrshire Breeders' Association as part of an aggressive program for breed improvement.

The Jersey breed has recently adopted a form of selective registration under the following stipulations.

Registration, as applied to purebred Jersey cattle, refers to the system whereby the pedigree and description of an animal, positively identified as the offspring of purebred parents, are recorded with The American Jersey Cattle Club. Because the parents of such an animal are themselves officially registered, as are their parents, in turn, the pedigree tracing back in an unbroken chain of purebreeding to the origin of the breed, the animal has always been considered eligible to receive the registration certificate. This certificate is the unquestioned credential of the animal's identity, proof positive of the purity of its breeding.

For many years, leading dairy cattle breeders advocated further requirements for registration—"to make the certificate mean something more than that the identified animal is of purebred parentage." They urged that proper consideration be given to whether the progenitors of an animal are of sufficient worth, from the standpoint of milk and butterfat production, to be perpetuated through their offspring. Selection of offspring, according to production talent of ancestors, has always been practiced voluntarily by progressive breeders of Jersey cattle. To this voluntary action can be attributed the great strides toward increased production and profit that has been made by the Jersey breed in America.

Research in production records of Jersey cattle proved the practical wisdom of making such selection compulsory. The American Jersey Cattle Club, after a careful survey of the breed, determined that Jersey breeders were prepared to take this important step. Enacted in June, 1939, the new regulations become operative January 1, 1942, giving all breeders ample time to conform with the requirements for "Selective Registration."

Selective registration will apply only to bulls of the Jersey breed. Although both parents contribute to the calf's inheritance of ability to produce profitably, it is axiomatic that "a good bull is half of the herd—a poor bull is all of the herd." Selective registration, therefore, aims gradually to eliminate from the Jersey breed all bulls of poor production pedigree by barring them from the official Herd Register.

The owner of a purebred Jersey bull calf will propose the animal for registration the same as heretofore. The same basic requirements will remain in force—that is, both sire and dam of the calf must first be registered by The American Jersey Cattle Club. That will establish the young bull's identity as a purebred Jersey. If such identity cannot be proved, the application must be rejected, of course, as in the past.

The second step in determining eligibility for registration requires examination of the production-transmitting history of the calf's sire, or of the records of butterfat production of the calf's dam. Only one of the following requirements must be satisfied to make the proposed animal eligible for registration:

If his sire is a "Proved Sire," whose daughters, tested in a Dairy Herd Improvement Association and reported to the U.S. Bureau of Dairying, averaged 400 pounds of butterfat in 305 days, the bull calf may be registered.

If his sire is a "Tested Sire" whose daughters, under official production test authenticated by the American Jersey Cattle Club, averaged 500 pounds of butterfat on a 365-day basis (mature equivalent) the bull calf may be registered.

If his dam has a record of 400 pounds of butterfat (305-day mature equivalent) in a Dairy Herd Improvement Association (as reported to the U.S. Bureau of Dairying) or in either of the A.J.C.C. production testing projects (the Herd Improvement Registry or the Register of Merit), or in the Canadian Government's Record of Performance, or in the Island of Jersey's Certificate of Merit, the bull calf may be registered.

If his sire is a "Star Bull," so identified by the special certificate awarded by The American Jersey Cattle Club, the bull calf may be registered.

Requirements and Scale of Credits for "Star Bull" Award

On the Sire's Side of the Pedigree

Sire	
If sire of bull to be starred is an A.J.C.C. Tested Sire with a 365-day mature equivalent average of:	450 lbs. butterfat, allow 1 earned credit toward "Star" award.
	500 lbs. butterfat, allow 2 earned credits toward "Star" award.
	550 lbs. butterfat, allow 3 earned credits toward "Star" award.
	600 lbs. butterfat, allow 4 earned credits toward "Star" award.
	650 lbs. butterfat, allow 5 earned credits toward "Star" award.
	700 lbs. butterfat, allow 6 earned credits toward "Star" award.
	750 lbs. butterfat, allow 7 earned credits toward "Star" award.

Credits	
If sire of bull to be starred has 10 classified daughters with an average score of:	81 per cent, allow 2 earned credits toward "Star" award. 82 per cent, allow 3 earned credits toward "Star" award. 84 per cent, allow 4 earned credits toward "Star" award.
If sire of bull to be starred is a son of an A.J.C.C. Tested Sire, with 365-day mature equivalent average of:	550 lbs. butterfat, allow 1 earned credit toward "Star" award. 600 lbs. butterfat, allow 2 earned credits toward "Star" award.

Transmitted credits

A "2-Star Bull" transmits 2 credits from his pedigree toward the "Star" award of his son.

A "3-Star Bull" transmits 4 credits from his pedigree toward the "Star" award of his son.

A "4-Star Bull" transmits 5 credits from his pedigree toward the "Star" award of his son.

NOTE.—If the earned credits from the sire's side of the pedigree exceed the transmitted credits, the transmitted credits are disregarded.

IMPORTANT.—At least one-third of credits toward a "Star" award must come from the sire's side of pedigree.

On the Dam's Side of the Pedigree

Dam	
If dam of bull to be starred has a Register of Merit or Herd Improvement Registry 365-day mature equivalent record of:	500 lbs. butterfat, allow 2 earned credits toward "Star" award. 600 lbs. butterfat, allow 3 earned credits toward "Star" award. 700 lbs. butterfat, allow 4 earned credits toward "Star" award.
Credits	
If dam of bull to be starred has been officially classified:	"Good Plus" (80 to 85%) allow 2 earned credits toward "Star" award. "Very Good" (85 to 90%) allow 3 earned credits toward "Star" award. "Excellent" (90% and over) allow 4 earned credits toward "Star" award.
If dam of bull to be starred is an A.J.C.C. Tested Dam with a 365-day mature equivalent average of:	450 lbs. butterfat, allow 1 earned credit toward "Star" award. 500 lbs. butterfat, allow 2 earned credits toward "Star" award. 550 lbs. butterfat, allow 3 earned credits toward "Star" award. 600 lbs. butterfat, allow 4 earned credits toward "Star" award. 650 lbs. butterfat, allow 5 earned credits toward "Star" award. 700 lbs. butterfat, allow 6 earned credits toward "Star" award.

If dam of bull to be starred is a daughter of an A.J.C.C. Tested Sire with 365-day mature equivalent average of:	500 lbs. butterfat, allow 1 earned credit toward "Star" award. 600 lbs. butterfat, allow 2 earned credits toward "Star" award.
If dam of bull to be starred is a daughter of an A.J.C.C. Tested Dam with a 365-day mature equivalent average of:	550 lbs. butterfat, allow 1 earned credit toward "Star" award. 600 lbs. butterfat, allow 2 earned credits toward "Star" award.
If sire of dam of bull to be starred has ten or more classified daughters with an average score of:	81 per cent, allow 1 earned credit toward "Star" award. 82 per cent, allow 2 earned credits toward "Star" award.

IMPORTANT.—At least one-third of credits toward a "Star" award must come from the dam's side of the pedigree.

Star Values of Pedigree Credits

The credits allowed in the above plan for Star Bulls must be translated into values that are readily understood. Each five credits are worth one star, thus:

* One-Star Bull—the summary of whose pedigree is not less than 5 credits. (At least two credits must come from the sire, and at least two credits from the dam.)

** Two-Star Bull—the summary of whose pedigree is not less than 10 credits. (At least four credits must come from the sire, and at least four credits from the dam.)

*** Three-Star Bull—the summary of whose pedigree is not less than 15 credits. (At least five credits must come from the sire, and at least five from the dam.)

**** Four-Star Bull—the summary of whose pedigree is not less than 20 credits, three or more of which must have been earned by classification. (At least seven of the 20 credits must have come from the sire, and at least seven from the dam.)

Jersey breeders said: "Give us a standard for evaluating young bulls so that we can talk about and advertise them in readily understood terms."

Buyers of Jersey bulls said: "Give us a simple and dependable method for determining the worth of a young bull as a future herd sire."

The Jersey breed has long been using standard designations for mature bulls tested and proved through their daughters' records of performance at the milk-pail. However, the supply of tested and proved Jersey bulls has never been sufficient to satisfy the demand. Owners of such animals prize them highly and price them accordingly. Often, new breeders and many veteran breeders who want to improve their established herds, cannot afford to purchase these highly desirable sires, even if the owners who developed them would be willing to sell.

Prospective buyers can, if they take the time, dig through the pedigrees of young bulls offered for sale. Unless they are experienced in such research, however, and understand the significance of each factor in the pedigree, they may become confused in the maze of information spread before them.

What was needed, therefore, was some nationally accepted measuring stick for young bulls, a convenient and dependable means of calling attention to their potential worth as future herd sires. The "Star Bull" method of recognizing the young bull's inherent talent for constructive breeding was evolved to solve the problem. The standard designations are in terms of "stars" which are officially awarded by The American Jersey Cattle Club on a special certificate. Depending upon the degree of achievement by the animal's parents and grandparents, from one to four stars may be awarded, each star being the equivalent of five credits in the pedigree.

The method recognizes both "earned credits" and "transmitted credits." Credits are "earned" through individual production records, Tested Sire and Dam averages, and classification. Credits are "transmitted" by Star Bulls from their pedigrees to their sons. Because a relationship is known to exist between production ability and conformation (type), due consideration is given to both factors in the assignment of the credits which are to be translated into "stars." The scale of credits appears on the previous pages:

Another recent development in the field of selective registration has been the formation of the American Dairy Cattle Club.[1] This is a recording society based entirely on records of production and pays no attention to external breed trade-marks; *i.e.*, any dairy cow of any breed or mixture of breeds can become a registered American Dairy Cattle animal (A.D.C.) upon meeting certain specifications as to production.

If a cow makes 300 lb. of butterfat or more (mature basis, 305-day twice-a-day milking) or has 2 daughters that make 300 lb. of butterfat, she can be listed in the *first order*.

If such a cow is bred to a bull with an index of 375 lb. or more (based on 5 or more unselected daughters) and the resulting daughter makes 350 lb. of butterfat, said daughter can be listed in the *second order*.

Likewise a bull whose dam made 300 lb. of butterfat (or had 2 daughters that did so) and whose sire had a minimum index of 375 lb. will, if he earns an index of 400 lb. or more on five or more unselected daughter-dam comparisons, be listed in the *second order*.

If a second-order cow is bred to a second-order bull and the resulting daughter makes 375 lb. of butterfat, said daughter can be listed in the *third order*.

[1] Since this is not a "pure breed" in the usual sense of that term, it will not be found listed among the pure breeds in Appendix B. The secretary is C. L. Clevenger and the address of The American Dairy Cattle Club is 11 South La Salle Street, Chicago, Ill.

Likewise a bull, whose sire and dam are listed in the second order, will, if he earns an index of 425 lb. or more on five or more unselected daughter-dam comparisons, be listed in the *third order*.

If a third-order cow is bred to a third-order bull and the resulting daughter makes 400 lb. of butterfat, said daughter can be listed in the *fourth order*.

Likewise a bull, whose sire and dam are listed in the third order, will, if he earns a minimum index of 450 lb., be listed in the *fourth order*.

Animals listed in the third and fourth orders are called *Registered A.D.C.* cattle. The following figure brings all the above specifications together.

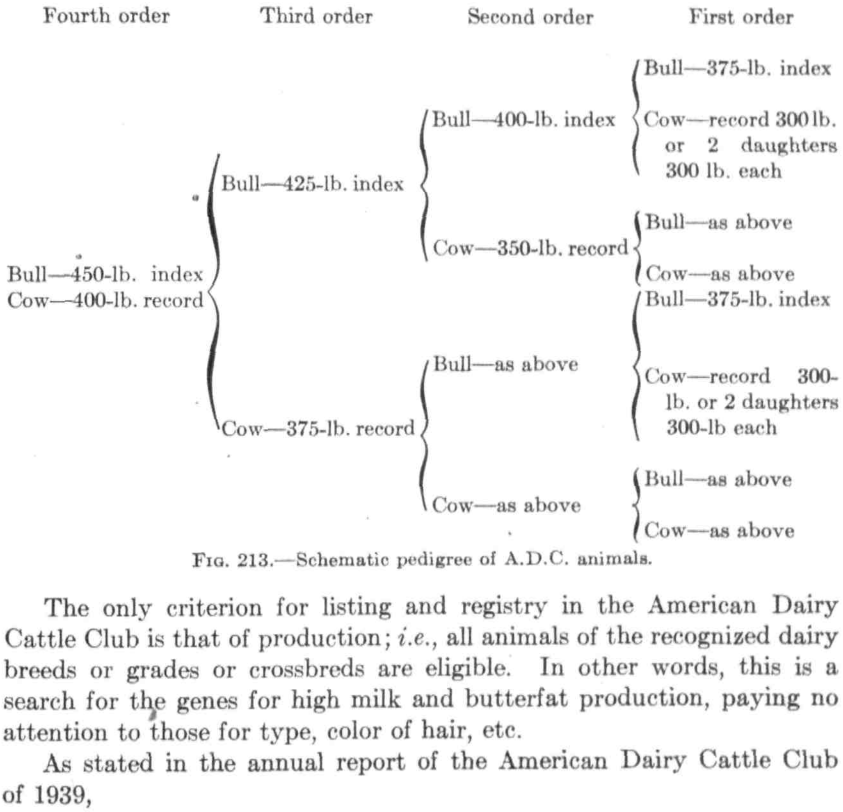

FIG. 213.—Schematic pedigree of A.D.C. animals.

The only criterion for listing and registry in the American Dairy Cattle Club is that of production; *i.e.*, all animals of the recognized dairy breeds or grades or crossbreds are eligible. In other words, this is a search for the genes for high milk and butterfat production, paying no attention to those for type, color of hair, etc.

As stated in the annual report of the American Dairy Cattle Club of 1939,

Our charges for these services to Associated Breeders are: Associated Breeder's fee—$15.00; identification fee, $1.00 per animal; testing fee—10¢ per cow in milk per month. This does not include the D.H.I.A. charges or the charge made by the various colleges of agriculture for supervising and reporting D.H.I.A. records. In many States the supervising charge is 50¢ per herd (of 30 animals)

per month. The cost of entering a herd of 30 cows and a bull in the work of this Club in such a State would be $82.00 the first year and $46.00 each succeeding year. These figures do not include D.H.I.A. charges, but include the supervising charge and the cost of identifying 10 calves per year after the first year. The breeder may initially select animals to be identified. We require that all identified animals be kept under continuous herd test with us, and that all offspring of identified females be in turn identified.

The services rendered are stated as follows:

Calculating his D.H.I.A. production records to the standard milking period basis, averaging the successive records of each cow, so calculated, and issuing cumulative certificates of pedigree and performance on each cow at the end of each lactation period; calculating his herd average on the same basis each year; calculating the indexes of his bulls and issuing similar certificates as each successive five pair index is completed; and comparing the indexes with such herd averages so that he can tell as fast as the information is available whether he is building his herd up or pulling it down. These we believe are services of basic importance to his existence as a dairy farmer. Some of them he could, but usually does not perform for himself. Most of them are not duplicated by the work of the Dairy Herd Improvement Associations, as supervised by the United States Department of Agriculture and the agricultural colleges.

In the same category of services to the breeder, we may mention the fact that our requirements stimulate him to qualify his animals for progressively higher orders of recording. Thus they give him encouragement to undertake or continue testing work, to use high-indexed bulls or the sons of such bulls, and to study his records in order to check the progress he is making up the ladder of our orders.

Far more important, however, is the fact that The American Dairy Cattle Club offers the means by which a number of breeders can work together in applying our breeding principles, and so makes it possible for each one to progress faster than he could working alone. The registry association principle has long been recognized as useful in the cooperative improvement of live stock. We offer registry association advantages to the breeders of unregistered cattle—a service which no other agency attempts to perform. Our system recognizes the fact that 80% of the D.H.I.A. cows in the country are unregistered, that it is extremely doubtful whether, with the same feed and care, there would be any difference between the producing ability of this 80% and the 20% that are registered, and that certainly many of the unregistered group are better than many of the registered group. We, therefore, do not require you to buy American cattle. We urge you to start with what you have in your barn and breed them up. When your animals have met our requirements, we then give currency to their worth by issuing our certificates of performance and pedigree (Recording Certificates) on them.

To the breeders of registered as well as unregistered cattle, we offer a sounder registry program than is made available to them by any other agency. Our program is the only one based on the standards in which the dairyman is primarily interested—namely, individual performance plus the ability to transmit

that performance. As a result, our certificates will in time carry a face value, and they will bring the price to which fair value is entitled.

In short, the service that we render to our breeder is to assist him to develop or improve the market for his surplus animals as breeding stock, and to produce his milk at lower cost, which he must do in order to stay in business under present conditions, and in order to earn a livelihood for himself and his family.

This is a very interesting experiment in a new type of registration based wholly on performance and opens up registration to grade and crossbred animals, as well as purebred, if they meet certain production requirements. The D.H.I. association member is already provided by the Bureau of Dairy Industry with the summarized records of his herd each year, his bulls are automatically proved and the information sent to him, and complete herd analysis is sent him when he has secured a succession of three proved bulls. No one would question the soundness of the basic idea on which the American Dairy Cattle Club is founded—proved performance. The principal drawback is that of cost. It costs about $30 to $50 a year at present to belong to a D.H.I. association. To belong to the American Dairy Cattle Club will cost an additional $40 to $50 per year. Only about 5 to 7 per cent of our dairy cattle are now in D.H.I. association work, and the main reason for this small percentage is that of cost. We need more cattle under test. Any plan that doubles the cost is not likely to swell the numbers. If anyone could devise a scheme that would halve the cost and double the numbers of cows tested he would indeed be a benefactor to the dairy industry.

Mention has been made earlier in this book of the Production Registry requirements for sows in the Duroc-Jersey and Hampshire breeds of swine.

In several European countries (Holland, Denmark, Switzerland) and on the Island of Jersey some form of selective registration has been practiced for many years. These systems vary from requiring the showing of animals at fairs to specific requirements in the way of production. The purpose, of course, is to try to rid the breeds of their undesirable genes.

The great expanse of the United States has made selective registration based on inspection of animals seem likely to prove so costly that no breeds have adopted such schemes as yet. The plan of the Jersey breed requiring some evidence of the probable ability to transmit high production on the part of bull calves was outlined above. Other breed associations are also considering the matter of selective registration.

Selective registration would presumably be based largely on records of performance. In other words, we must get the records before we can have selective registration. Actually we may find that, when we get the records on our breeding animals and give them wide publicity,

we will not need selective registration because the records themselves serve this purpose. It is obvious that some progress would ensue if a breed were able to discard a certain fraction of its poorest animals each year. Figure 100 on page 374 is a graph of 705 Holstein bulls that are indexed in Volume 11 of the "Holstein-Friesian Red Book." Presumably a breeder would not choose a son of one of those proved bulls with an index of 6,000 lb. of 3.5 per cent milk, so that in this way the publication of facts should help to eliminate the poorer genes in the breed, which is what selective registration is designed to do. If the breed associations said arbitrarily, we will not register any more offspring of the bulls in the lowest 20 per cent of the graph (Fig. 100), some 157 bulls would lose their standing as registered bulls. This would seem a sensible thing to do after an animal had demonstrated its poor breeding qualities, but from a practical standpoint there are many angles to the problem. A procedure of this sort would in effect amount to the same thing as selective registration.

Many breeds list certain disqualifying characters, but these generally concern such things as color, the freemartin until she has proved her fertility, etc., and have nothing to do with efficient production. Also in the dairy-breed herd-classification plans a breeder agrees to relinquish the registration of animals classified as *poor*, and females classified as *fair* can no longer have their male calves registered. Likewise in breed herd testing the production of the poorest animals is omitted from the breeder's herd average, provided he surrenders their registration certificates.

It seems unlikely that selective registration on the European model will be generally adopted by American breed associations.

Now that the necessity for more complete records in all classes of livestock is being recognized, we can expect the breed associations to busy themselves with plans for securing them. It is probably realized that the breed which supplies its breeders with the most accurate and complete records of breeding accomplishments by the animals in the breed will be the one to make the most rapid progress in eliminating poor genes, and thus selective registration will be accomplished in an indirect manner.

In addition to the opportunities for animal improvement that exist in the cooperative work of all members of a breed association, there are other cooperative efforts which are beginning to yield results. Among these the best known and most extensive are the dairy herd improvement associations. This work was started in 1906, and in 1941 there were 1,383 of these associations with approximately 31,381 members and 763,502 cows under test. The value of this type of cooperative endeavor has been abundantly proved and sufficiently chronicled in other places.

The same may be said for bull associations, or bull circles. These associations are generally made up of three to five blocks or stations. Three dairymen, for instance, may pool their resources and purchase three bulls, so that instead of one man owning one bull which he will have to replace in 2 or 3 years to avoid inbreeding, each man owns one-third interest in three bulls. Each man takes one of the three bulls to his own farm and uses him for 2 years, then a triple exchange is made according to a prearranged plan and the process repeated at the end of another 2 years. In this way a man provides himself with bull service for 6 years instead of 2 by his original purchase. If three sons of some meritorious bull are secured to start with, an automatic system of line-breeding is set up. In addition, all the bulls are kept alive until proved, and those that prove good can be continued in service, the others sent to the butcher. Like the D.H.I.A. work, the bull-association idea has fully proved its merit.

Among the newer cooperative efforts in breeding are the artificial-inseminating associations and the herd-health associations. Artificial insemination has grown rapidly in the past 3 years, and its continued growth seems probable. It is of particular advantage to the small breeder, for it gives him at no greater cost the use of a much better sire than he could own individually. Like the bull-association plan, it can automatically give rise to linebreeding on a community basis without the risk of intensifying undesirable characters through too close breeding.

The herd-health idea can be worked out separately or in conjunction with artificial breeding. The following is the herd-health portion of the combined plan recently put into operation by dairymen in Plymouth and Norfolk Counties in Massachusetts under the leadership of the county farm bureaus and the county agents, J. T. Brown of Plymouth County and Earl M. Ricker of Norfolk County.

Herd Health Service Agreement
of the
Dairy Breeding and Herd Health Service Unit of the Plymouth County Farm Bureau

This agreement made and entered into this______day of__________, 19___ of________________, Mass., by and between the Dairy Breeding and Herd Health Service Unit of the Plymouth County Farm Bureau, represented by its official veterinarian, Dr. Chester Harden, and____________________
(Member)

WITNESSETH:

The member agrees to the following:

1. That he will become a member of the Plymouth County Farm Bureau by paying a membership fee of $6 due November 1st annually.

2. That he will enroll______(number) cows representing the total number of animals of breeding age in the herd at the time of this agreement for Herd Health Service at the rate of ($1.00) one dollar per head, or a total of________dollars ($ for a six months' period payable to the veterinarian at the first service visit.

The Unit agrees to provide the following services;

1. Regular examinations of cows not bred, with a study of the breeding history of each cow.
2. Examination of pregnancy as soon as possible after breeding, the minimum period to be 60 days.
3. Treatment of abnormal conditions of the genital tract with the exception of retained placenta.
4. Taking of blood samples twice a year for the Bang's test, and preparing for shipment to laboratory, for those who request it.
5. Vaccinating of calves to immunize against Bang's disease at request of owner.
6. Examination of bulls, physically and their semen microscopically if requested.
7. Prevention and control of common ailments:
   a. *Mastitis;* Classification of herd according to infection present and advice on proper procedure for control as outlined in the Extension Service program.
   b. Prescribe treatment for general health and to treat for foot rot, barn itch, lice, and other minor ailments, and to instruct the farmer in additional treatments.
   c. Care of young calves, including management for prevention of white scours, calf pneumonia, and hemorrhagic septicemia, and treatment for removal of horn buttons and extra teats.
   d. To administer all necessary and approved vaccines and serums to aid in the control of disease. The veterinarian shall furnish at reasonable cost (cost plus 15¢) per animal all medicines and vaccines used by him when making regular monthly examinations.

We hereby mutually agree.

Signed: Date________ __________________Member

Date________ __________________Veterinarian

For the Dairy Breeding and Herd Health Unit

Along with the above a dairyman may, if he wishes, have the convenience of artificial breeding under the following stipulations:

1. *Artificial Breeding* is available from superior sires of the Holstein, Guernsey, Ayrshire and Jersey Breeds.
   A. Fees for artificial insemination
      First service $6.00 paid to veterinarian.
      First re-breeding (if necessary)—free.
      Additional re-breedings $3.00 each.
      Members with less than 4 cows may pay $7.50 for each initial service without paying membership fee.
   B. Pregnancy diagnosis at request of owner at regular breeding call after 60 days following service.
   C. Examination and physical treatment for reproductive health of other cows, not to exceed $1 per cow or $10 per herd.

The past 20 or 30 years have furnished the basic scientific principles in terms of reproductive physiology, hereditary transmission, and the control of genital diseases for a sound art of animal breeding. Coopera-

tive efforts among breeders are providing the practical working organizations for putting these scientific discoveries into effect.

Many agencies are now cooperating in livestock-improvement endeavor. The Bureau of Animal Industry "Better Sires—Better Stock" campaign has been instrumental in ridding several whole counties of grade and scrub sires. In many states the extension service working through the county agents is carrying on detailed programs of grading, selection, and culling in all types of livestock, and in some states the college or university is loaning sires to cooperating groups of producers. These projects involve the securing and intelligent appraisal of actual transmitting performances, and many of them involve county and district shows with special attention given to "get of sire" classes. In some states county livestock-improvement associations have been formed, and in addition to livestock improvement through the testing of sires and the greater use of proved sires, grading and management demonstrations and competitive showing, such things as "livestock protective associations" and "cooperative grazing associations" are developing. Such cooperative efforts of producers are in many instances being aided by banks, stockyard companies, railroads, civic clubs, etc.

Regional laboratories for livestock improvement have been established by the Bureau of Animal Industry and the Bureau of Dairy Industry, in addition to the National Agricultural Research Center at Beltsville, Md., to cope with the problem of analyzing our present breeding animals and to devise methods through systems of breeding and selection for rendering them pure in their inheritance for commercially desirable qualities. Last, but by no means least, our breed associations are devising projects aimed at discovering the best in each respective breed and are beginning to foster plans to weed out the poor purebreds.

The two major problems that still confront the breeding and improvement of livestock can be solved only by proving sires and by creating viable and desirable inbred strains to be used either as homozygous "pure lines" or in crosses among themselves, "controlled heterozygosity." The graph shown as Fig. 100 on page 374 shows the distribution of 705 indexed Holstein-Friesian bulls. A lot of these bulls are poor, most of them are average, and a few are exceptionally good. In other words, in Holsteins we are generally breeding average bulls to average cows, from which, of course, the only logical expectation is that we will get average offspring. There is no reason to suspect, if we had the breeding data on all the males in use in all the other classes and breeds of livestock, that we would get any different sort of picture.

Since our animal populations in their commercially important features probably simulate a normal curve genetically, the task of the livestock industry is to devise procedures that will reveal the facts about our

animals so that those with the better gene complexes may be used in breeding operations and the poorer ones discarded. Since the amount of culling that can be practiced with females is decidedly limited, *i.e.*, we could not overnight dispose of 50 per cent of our dairy cows, desirable as that might be from a genetic standpoint, provided we knew which ones to discard, the problem must be solved largely in terms of males. The procedure both for the industry as a whole and for the individual breeder is obvious. It consists of testing out and proving by means of records of performance of their offspring many times the number of males now being proved. Only in this way can the best males from a genetic standpoint be discovered. When they have thus been discovered, both they and their proved good sons should be used extensively, which probably means the wider adoption of the technique of artificial insemination.

The other major problem is that of carrying on intensive inbreeding experiments on a large enough scale so that they may have a fair chance of being successful. This the individual breeder is generally not equipped to do. The regional animal-breeding laboratories sponsored by the U.S. Department of Agriculture and the individual states are now at work on this problem. If enough strains can be started in closebreeding, a few of them can probably be carried through until they emerge after a few generations as relatively pure strains. Experimental crossing of such strains with the purpose of bolstering the weak points of each can perhaps lead eventually to relatively pure-breeding lines in animals, at least in a degree comparable with those already created in plants. There are many difficulties involved in such a program, but they would not at this time seem to be insurmountable. If such "pure lines" can be created and sires made available to breeders to be used in artificial-breeding associations, or in bull, boar, ram, or stud associations, and if the individual breeder will keep such records as will enable him to select intelligently in his best female lines, animal breeding will begin to approach a scientific level. As pointed out by Dr. Hugh C. McPhee, what we seek in our breeding animals is *merit*. Genetically, this can be achieved either through homozygosity or perhaps, as in the case of corn breeding, through controlled heterozygosity.

Not so many years ago animal breeding was thought by many to involve a considerable amount of magic, which could be invoked by only a select few on the basis of a God-given instinct. Genetics has dispelled this myth and made it evident that anyone who is willing to take the pains to analyze his animals in terms of their producing and transmitting abilities can also use, with varying degrees of success to be sure, the only tools which ever have been or will be available for animal improvement—breeding systems and selection.

A proton and electrons, then elements emerge—
They organize and synthesize to form a living surge.
Then animals and man appear in orderly progression:
Teamed, they move with quickened pace— a fitting, joint possession.

APPENDIX A

Further References to Inheritance Studies in Animals

The following references are arranged chronologically so that the most recent work in any character may be more easily found. Many of these papers carry extended bibliographies.

An excellent exercise for students consists in the forming of lists of inherited characters in each of the classes of livestock.

Horses

From Journal of Heredity:

ANDERSON, W. S. 1914. Coat Color in Horses, **5**(11): 482–488, November.

McCANN, L. P. 1916. Sorrel Color in Horses, **7**(8): 370–372, August.

LOYD-JONES, O. 1916. Mules that Breed, **7**(11): 494–502, November.

BUSH-BROWN, H. K. 1920. Heredity in Horses, **11**(5): 215–227, May–June.

GONZALEZ, B. M., and VILLEGAS, V. 1928. "Bighead" of Horses; A Hereditable Disease, **19**(4): 159–168, April.

KLEMOLA, V. 1933. The "Pied" and "Splashed White" Pattern in Horses and Ponies, **24**(2): 65–69, February.

BLUNN, C. T., and HOWELL, C. E. 1936. The Inheritance of White Facial Markings in Arabian Horses, **27**(8): 293–299, August.

PRAWOCHENSKI, R. 1936. A New Lethal Factor in the Horse, **27**(11): 411–414, November.

ANDERSON, W. S. 1939. Fertile Mare Mules, **30**(12): 549–551, December.

CASTLE, W. E. 1940. The Genetics of Coat Color in Horses, **31**(3): 127–128, March.

SALISBURY, G. W. 1941. Inheritance of Equine Coat Color, **32**(7): 235–239, July.

——— and BRITTON, J. W. 1941. The Inheritance of Equine Coat Color, **32**(8): 255–260, August.

From Journal of Genetics:

STURTEVANT, A. H. 1912. A Critical Examination of Recent Studies on Colour Inheritance in Horses, **2**(2): 41–52, February.

ROBB, R. C. 1935. A Study of Mutations in Evolution: I. Evolution in the Equine Skull, II. Ontogeny in the Equine Skull, **31**(1): 39–52, June.

Cattle

From Journal of Heredity:

PETERS, J. 1914. Inheritance of Milk Yield, **5**(1): 18, January.

HANSSON, N. 1914. Increasing Richness of Milk, **5**(4): 184, April.

KRAEMER, H. 1914. Effects of Inbreeding, **5**(5): 226–234, May.

MARSHALL, F. R. 1914. Holstein Milk Yield, **5**(10): 437–439, October.

KUHLMAN, A. H. 1915. Black and White Ayrshires, **6**(7): 314–322, July.

WENTWORTH, E. N. 1916. Sex in Livestock Breeding, **7**(1): 29–32, January.

WRIGHT, S. 1917. Color Inheritance in Mammals, **8**(11): 521–527, November.

Cole, L. J. 1919. A Defect of Hair and Teeth in Cattle Probably Hereditary, **10**(7): 303–307, October.

Gowen, J. W. 1920. Inheritance in Crosses of Dairy and Beef Breeds of Cattle, **11**(7): 300–316, September–October, 1920, and also **11**(8): 365–378, November–December.

Castle, W. E., and Wachter, W. L. 1921. Genetics of Hereford Cattle, **12**(1): 37–39, January.

Kuiper, K. 1921. Color Inheritance in Cattle, **12**(3): 102–109, March.

Lush, K. 1922. An Hereditary Notch in the Ears of Jersey Cattle, **13**(1): 8–13, January.

Hayden, C. C. 1922. A Case of Twinning in Dairy Cattle, **13**(1): 22–24, January.

Templeton, G. S. 1923. Unusual Color Inheritance, **14**(10): 39–40, April.

Duck, R. W. 1923. Colors of Shorthorn Cattle, **14**(2): 65–75, May.

Dunn, L. C., Webb, H. F., and Schneider, M. 1923. The Inheritance of Degrees of Spotting in Holstein Cattle, **14**(5): 229–240, August.

Wright, S. 1923. Mendelian Analysis of Pure Breeds of Livestock, Duchess Shorthorns, **14**(9): 405–421, December.

Lush, J. L. 1924. Twinning in Brahma Cattle, **15**(1): 25–28, January.

———. 1924. Double Ears in Brahma Cattle, **15**(2): 93–96, February.

Smith, A. D. B. 1925. Shorthorn Colors, **16**(3): 73–84, March.

Lush, R. H. 1925. Inheritance of Twinning in Cattle, **16**(8): 273–279, August.

Gowen, J. W. 1926. Heredity and Milk Yield, **17**(5): 185–186, May.

McPhee, H. C., and Wright, S. 1926. Mendelian Analysis of the Pure Breeds of Livestock; British Dairy Shorthorn, **17**(11): 397–402, November.

Churchill, O. O. 1927. Sex and Horns in Cattle, **18**(6): 278–280, June.

Horlacher, W.R 1928. Exceptional Color Inheritance in Hereford Cattle, **19**(1): 10–11, January.

Lush, J. L. 1929. Atavism in Jersey Cattle, **20**(8): 381–383, August.

———. 1929. Identical Twins in Jersey Cattle, **20**(11): 511–513, November.

———. 1930. "Ducked Legged" Cattle on Texas Ranges, **21**(2): 85–90, February.

Heizer, E. E. 1932. An Inherited Udder Abnormality in Cattle, **23**(3): 111–114, March.

Becker, R. B. 1933. Recessive Coloration in Dutch Belted Cattle, **24**(7): 283–287, July.

Rhoad, A. O. 1933. Restricted Extension Color Factor in Zebu Cattle, **24**(7): 347–348, July.

Hutt, F. B. 1934. A Hereditary Lethal Muscle Contractive in Cattle, **25**(1): 41–46, January.

Cole, L. J., Van Lone, E. E., and Johansson, I. 1924. Albinotic Dilution of Color in Cattle, **25**(4): 145–156, April.

Craft, W. A., and Blizzard, W. L. 1934. Inheritance of Semi-Hairlessness in Cattle, **25**(10): 385–390, October.

White, W. T., and Ibsen, H. L. 1935. Color Inheritance in Galloway-Holstein, **26**(2): 75–84, February.

———. 1934. Inherited Susceptibility to Acute Mastitis in Cattle, **25**(12), 489–490, December.

Atkeson, F. W., and Warren, T. R. 1935. Inheritance of Wrytail in Jersey Cattle, **26**(8): 331–334, August.

Regan, W. M., Mead, S. W., and Gregory, P. W. 1935. An Inherited Skin Defect in Jersey Cattle, **26**(9): 357–362, September.

Wipprecht, C., and Horlacher, W. R. 1935. A Lethal Gene in Jersey Cattle, **26**(9): 363–368, September.

LUSH, J., HOLBERT, J. C., and WILLIAMS, O. S. 1936. Genetic History of Holstein-Friesian Cattle in the U.S., **27**(2): 61–72, February.

RHOAD, A. O. 1936. The Silver Gray Color in Indian Cattle, **27**(3): 113–119, March.

LUSH, J. 1936. Genetics and Animal Breeding (Review), **27**(5): 201–205, May.

KNAPP, B., EMMEL, M. W., and WARD, W. F. Inheritance of Screwtail in Cattle, **27**(7): 269–271, July.

HEIZER, E. E., and HERVEY, M. C. 1937. Impacted Molars—A New Lethal in Cattle, **28**(3): 123–127, March.

YODER, D. M., and LUSH, J. L. 1937. A Genetic History of the Brown Swiss in the U.S., **28**(4): 154–160, April.

ROBERTS, E. 1937. Color Inheritance in Shorthorn Cattle, **28**(5): 167–168, May.

GUILBERT, H. R. 1937. What Causes "Black-Cutter" Beef, **28**(6): 213–214, June.

WILLIAM, O. S. 1937. A Genetic History of Hereford Cattle in the U.S., **28**(8): 283–294, August.

LUSH, J. L. 1937. Identical Twins in Cattle, **28**(12): 415–419, December.

KANS. AGR. EXPT. STA. 1937. Inheritance of Horns and Color in Cattle, **28**(12): 420, December.

BONNIER, G., and SKARMAN, S. 1938. Aids to the Identification of Monozygotic Twins in Cattle, **29**(7): 269–272, July.

SHAW, A. O. 1938. A Skull Defect in Cattle, **29**(8): 319–320, August.

ELY, F., HULL, F. E., and MORRISON, H. B. 1939. Agnathia, a New Bovine Lethal, **30**(3): 105–108, March.

BUSHNELL, R. J. 1940. Color Genes in Holstein-Friesian by Brown Swiss Crosses, **31**(5): 253–256, May.

BRANDT, G. W. 1941. Achondroplasia in Calves, **32**(6): 183–186, June.

From Journal of Genetics:

WRIEDT, O. 1919. The Brindle Colour in Cattle in Relation to Red, **9**(1): 83–84 December.

PITT, F. 1920. Notes on the Inheritance of Colour and Markings in Pedigree Hereford Cattle, **9**(3): 281–304, February.

WATSON, S. A. S. 1921. A Mendelian Experiment with Aberdeen-Angus and West Highland Cattle, **11**(1): 59–68, April.

ROBERTSON, E. 1921. Notes on Breeding for Increase of Milk in Dairy Cattle, **11**(1): 79–90, April.

SMITH, A. D. B. 1927. The Inheritance of Horns in Cattle, Some Further Data, **18**(3): 365–374, August.

MOHR, O. L., and WRIEDT, C. 1928. Hairless, a New Recessive Lethal in Cattle, **19**(3): 315–336, May.

WRIEDT, C., and MOHR, O. L. 1928. Amputated, a Recessive Lethal in Cattle: With a Discussion on the Bearing of Lethal Factors on the Principles of Livestock Breeding, **20**(2): 187–216, November.

WRIEDT, C. 1930. The Inheritance of Butterfat Percentage in Crosses of Jerseys with Red Danes, **22**(1): 45–64, April.

MOHR, O. L., and WRIEDT, C. 1930. Short Spine, a New Recessive Lethal in Cattle: With a Comparison of the Skeletal Deformations in Short-spine and in Amputated Calves, **22**(2): 279–298, May.

WHITE, W. T., and IBSEN, H. L. 1936. Horn Inheritance in Galloway-Holstein Cattle Crosses, **32**(1): 33–50, February.

PUNNETT, R. C. 1936. The Experiments of T. H. Riches Concerning the Production of Monsters in Cattle, **32**(1): 65–72, February.

BOGART, R., and IBSEN, H. L. 1937. The Relation of Hair and Skin Pigmentation to Colour Inheritance in Cattle, with some Notes on Guinea-pig Hair Pigmentation, **35**(1): 31–60, October.

ANNETT, H. E. 1939. Notes on a New Recessive Lethal in Cattle, **37**(2): 301–302, February.

From Genetics:

GOWEN, J. W. 1920. Studies in Milk Secretion V: On the Variations and Correlations of Milk Secretion with Age, **5**(2): 111–188, August.

GOWEN, J. W. 1926. Studies in Milk Secretion VI: On the Variations and Correlations of Butterfat Percentage with Age in Jersey Cattle, **5**(3): 249–324, September.

CAMPBELL, M. H. 1924. Inheritance of Black and Red Coat Colors in Cattle, **9**(5): 419–441, December.

GREGORY, P. W. 1933. The Nature of Size Factors in Domestic Breeds of Cattle, **18**(3): 221–249, May.

GOWEN, J. W. 1933. On the Genetic Constitution of Jersey Cattle, as Influenced by Inheritance and Environment, **18**(5): 415–440, September.

IBSEN, H. L. 1933. Cattle Inheritance I: Color, **18**(5): 441–480, September.

Sheep

From Journal of Heredity:

RITZMAN, E. G. 1920. Breeding Earless Sheep, **11**(5): 238–240, May–June.

WRIEDT, CHR. 1924. Breeding Earless Sheep, **12**(2): 56, February.

DUCK, R. W. 1922. Mendelism in Fur Sheep, **13**(2): 63–68, February.

CASTLE, W. E. 1924. The Genetics of Multinippled Sheep, **15**(2): 75–85, February.

WRIEDT, CHR. 1924. The Gromet Pattern in Sheep, **15**(3): 125–127, March.

SPOTTEL, W. 1926. Inheritance of Wool Characteristics (Review), **17**(1): 27–30, January.

WASSIN, BORIS. 1931. Linkage Studies in Sheep, **22**(1): 9–13, January.

WARWICK, B. L., and DUNKLE, P. B. 1939. Inheritance of Horns in Sheep, **30**(8): 325–329, August.

CARTER, R. C. 1940. A Genetic History of Hampshire Sheep, **31**(2): 89–93, February.

IBSEN, H. L., and COX, R. F. 1940. Inheritance of Horns and Scurs in Sheep, **31**(7): 327–336, July.

CASTLE, W. E. 1940. Genetics of Horns in Sheep, **31**(11): 487–489, November.

BERRY, R. O. 1941. The Chromosome Complex of Domestic Sheep, **32**(8): 261–267, August.

From Journal of Genetics:

ROBERTS, S. A. F. 1926. Color Inheritance in Sheep, II: The Piebald Pattern of the Piebald Breed, **17**(1): 77–84, August.

ROBERTS, S. A. F. 1928. Color Inheritance in Sheep, III: Face and Leg Color, **19**(2): 261–268, January.

ROBERTS, S. A. F. 1929. The Inheritance of a Lethal Muscle Contracture in Sheep, **21**(1): 57–70, April.

ROBERTS, S. A. F., and WHITE, R. G. 1930. Color Inheritance in Sheep, IV: White Color, Recessive Black Color, Recessive Brown Color, Badger-face Pattern, and Reversed Badger Face Pattern, **22**(2): 165–180, May.

ROBERTS, S. A. F., and WHITE, R. G. 1930. Color Inheritance in Sheep, V: Prominent Black, **22**(2): 181–190, May.

ROBERTS, S. A. F. 1931. Color Inheritance in Sheep, VI: The Genetic Constitution of the Wild Mouflon, **25**(1): 1–16, November.

GREGORY, P. W., MILLER, R. F., and STEWARD, M. A. 1940. An Analysis of Environmental and Genetic Factors Influencing Stomach-worm Infestation in Sheep, **39**(3): 391–400, March.

Goats

From Journal of Heredity:

LUSH, J. L. 1926. Inheritance of Horns, Wattles and Color in Goats, **17**(3): 73–90, March.

ASDELL, S. A., and SMITH, A. D. B. 1928. Inheritance of Color, Beard, Tassel, and Hair in the Goat, **19**(9): 425–430, September.

LUSH, J. L. 1930. Nervous Goats, **21**(6): 243–247, June.

KISLOVSKY, D. 1937. Inherited Hairlessness in Goats, **28**(8): 265–267, August.

EATON, O. N., SIMMONS, V. J. 1939. Hermaphrodism in Milk Goats, **30**(6): 257–260, June.

From Journal of Genetics:

ASDELL, S. A., and CREW, F. A. E. 1925. The Inheritance of the Horn in the Goat, **15**(3): 367–374, July.

Swine

From Journal of Heredity:

FROHLLICH, G. 1914. Color Inheritance in Pigs, **5**(2): 92, February.

WENTWORTH, E. N., and AUBEL, C. E. 1916. Inheritance of Fertility in Swine, **7**(5): 224, May.

SEVERSON, B. O. 1917. Color Inheritance in Swine, **8**(8): 379–381, August.

WRIGHT, S. 1918. Color Inheritance of Mammals: Swine, **9**(1): 33–38, January.

LUSH, J. L. 1921. Inheritance in Swine, **12**(2): 57–70, February.

CREW, F. A. E. 1924. Blue and White Color in Swine, **15**(9): 395–396, September.

MCPHEE, H. C., and ZELLER, J. H. 1925. Unusual Coat Colors in Swine, **16**(9): 347–349, September.

WARWICK, B. L. 1926. Inheritance of Black in Swine, **17**(7): 251–254, July.

NORDBY, J. E. 1930. Congenital Ear and Skull Defects in Swine, **21**(12): 499–501, December.

ROBERTS, E., and CARROLL, W. E. 1931. The Inheritance of Hairlessness in Swine, **22**(4): 125–132, April.

NORDBY, J. E. 1932. Inheritance of Whorls in the Hair of Swine, **23**(10): 397–404, October.

HUGHES, E. H., and HART, H. 1934. Defective Skulls Inherited in Swine, **25**(3): 111–115, March.

NORDBY, J. E. 1934. Kinky Tail in Swine, **25**(4): 171–174, April.

MCPHEE, H. C., and BUCKLY, S. S., 1934. Inheritance of Cryptorchidism, **25**(8): 295–303, August.

RHOAD, A. O. 1934. Woolly Hair in Swine, **25**(9): 371–374, September.

NORDBY, J. E. 1934. Congenital Defects in the Mammae of Swine, **25**(12): 499–502, December.

HODGSON, R. E. 1935. An Eight Generation Experiment in Breeding Swine, **26**(5): 209–217, May.

HUGHES, E. H. 1935. Polydactyly in Swine, **26**(10): 415–418, October.

HENKE, L. A. 1935. Is Fecundity in Swine Inherited, **26**(11): 455–456, November.

Blunn, C. I., and Hughes, E. H. 1938. Hydrocephalus in Swine, **29**(5): 203–208, May.

Annett, H. E. 1938. A New Ear Defect in Pigs, **29**(12): 469–470, December.

Freeman, V. A. 1939. Varieties in the Number of Vertebrae of Swine, **30**(2): 61–64, February.

Lush, J. L., and Anderson, A. L. 1939. A Genetic History of Poland-China Swine, **30**(4): 149–156, April; **30**(5): 219, 224, May.

Nordby, J. E. 1939. Inequalities in the Digits in Swine, **30**(7): 307–310, July.

Berge, S. 1941. The Inheritance of Paralyzed Hind Legs, Scrotal Hernia and Atresia Ani in Pigs, **32**(8): 271–275, August.

From Genetics:

Lush, J. L., Hetzur, H. O., and Culbertson, C. C. 1934. Factors Affecting Birth Rates of Swine, **19**(4): 329–343, July.

Miscellaneous Mammals

From Journal of Heredity:

Little, C. C. 1914. Coat Color in Pointer Dogs, **5**(6): 244–248, June.

Simpson, Q. I. 1914. Coat Pattern in Mammals, **5**(8): 329–339, August.

Barrows, W. M., and Phillips, J. 1915. Color in Cocker Spaniels, **7**(9): 387–397, September.

Castle, W. E., and Wright, S. 1916. Studies of Inheritance in Guinea Pigs, **7**(12): 540, December.

Wright, S. 1917. Color Inheritance in Mammals, **8**(5): 224–235, May.

———. 1917. Color Inheritance in the Mouse, **8**(8): 373–378, August.

———. 1917. Color Inheritance in the Rat, **8**(9): 426–430, September.

———. 1917. Color Inheritance in the Rabbit, **8**(10): 473–475, October.

———. 1917. Color Inheritance in the Guinea Pig, **8**(10): 476–480, October.

———. 1918. Color Inheritance in the Dog, **9**(2): 87–90, February.

———. 1918. Color Inheritance in the Cat, **9**(3): 139–144, March.

Hunt, H. R., and Wright, S. 1918. Pigmentation in Guinea Pig Hair, **9**(4): 178–181, April.

Lush, J. L. 1930. How Farm Animals Inherit, **21**(7): 306–308, July.

Wright, S. 1934. Polydactylous Guinea Pigs, **25**(9): 359–362, September.

Keeler, C. E., and Castle, W. E. 1934. Blood Group Inheritance in Rabbits, **25**(11): 433–439, November.

Eaton, O. N. 1937. A Hereditary Eye Defect in Guinea Pigs, **28**(10): 253, October.

From Journal of Genetics:

Punnett, R. C. 1912. Inheritance of Coat Color in Rabbits, **2**(3): 221–238, November.

Punnett, R. C. 1915. Further Experiments on the Inheritance of Coat Color in Rabbits, **5**(1): 37–50, July.

Punnett, R. C., and Bailey, P. G. 1918. Genetic Studies in Rabbits, I. On the Inheritance of Weight, **8**(1): 1–26, December.

Onslow, H. 1922. A Note on the Inheritance of the "Steel" Coat-Color in Rabbits, **12**(1): 91–100, April.

Salaman, R. N. 1922. The Inheritance of Fur Types and Hair Characters in Rabbits, **12**(2): 179–208, October.

Punnett, R. C., and Pease, M. S. 1925. On the Pattern of the Dutch Rabbit, **15**(3): 375–412, July.

Punnett, R. C. 1926. The Dutch Rabbit—Castle, Pease and Punnett, **16**(2): 197–200, January.

Castle, W. E. 1926. On the Pattern of the Dutch Rabbit, a Discussion of the Results of Punnett and Pease, **16**(2): 189–196, January.

Punnett, R. C. 1928. Further Notes on Dutch and English Rabbits, **20**(2): 247–260, November.

Pease, M. S. 1928. Experiments on the Inheritance of Weight in Rabbits, **20**(2): 261–310, November.

Marchlewski, T. 1934. Two Cases of Reverse Mutations in the Color Factors of Rabbits, **29**(1): 153–158, April.

From Genetics:

Ibsen, H. L., and Bushnell, L. D. 1934. The Effects Produced on Parents and Descendants by the Injection of Calf Lens Material Directly into the Rabbit Parent, **19**(4): 293–309, July.

Castle, W. E., and Reed, S. P. 1936. Studies in Inheritance in Lop-eared Rabbits, **21**(4): 297–309, July.

APPENDIX B

Livestock Record Associations

The following list of livestock record associations, as of Sept. 1, 1941, is presented through the courtesy of Mr. Ellis MacFarland, secretary of the National Society of Livestock Record Associations with headquarters at the Union Stock Yards, Chicago, Ill. This society was organized in 1911 and represents over 350,000 breeders of purebred livestock. The purposes of the society are stated as follows:

"The objects of this Society shall be to advance the interests of member registry associations, (1) by devising and perfecting methods for preserving pedigrees of purebred animals; (2) by endeavoring to secure the enactment of equitable laws relating to the purebred livestock industry and to livestock record associations; (3) by securing the adoption of just freight and express rates on exhibition and breeding stock; and (4) by originating or participating in any and all other activities which will in the judgment of the Directors of the Society advance the interests of breeders of purebred livestock through their respective registry associations.

Beef and Dual-purpose Cattle

American Aberdeen-Angus Breeders Association, 1 Dexter Park Avenue, Union Stock Yards, Chicago, Ill., W. H. Tomhave, Secretary.

American Brahman Breeders' Association, Hungerford, Tex., Mrs. S. C. Border, Secretary.

American Devon Cattle Club, Inc., Meredith, N.H., W. J. Neal, Secretary.

American Galloway Breeders' Association, 840 Exchange Avenue, Union Stock Yards, Chicago, Ill., Miss Margaret Coridan, Secretary.

American Hereford Cattle Breeders' Association, 300 West 11th Street, Kansas City, Mo., R. J. Kinzer, Secretary.

American Polled Hereford Breeders' Association, 712 Old Colony Building, Des Moines, Iowa, B. O. Gammon, Secretary.

American Shorthorn Breeders' Association, 1 Dexter Park Avenue, Union Stock Yards, Chicago, Ill., H. J. Gramlich, Secretary.

American Polled Shorthorn Society, 1 Dexter Park Avenue, Union Stock Yards, Chicago, Ill., Miss Emily Krahn, Secretary.

The Milking Shorthorn Society, 1 Dexter Park Avenue, Union Stock Yards, Chicago, Ill., W. J. Hardy, Secretary.

Dairy Cattle

American Guernsey Cattle Club, Peterboro, N.H., Karl B. Musser, Secretary.

American Jersey Cattle Club, 324 West 23rd Street, New York, N.Y., L. W. Morley, Secretary.

Ayrshire Breeders' Association, Brandon, Vt., C. T. Conklin, Secretary.

Brown-Swiss Cattle Breeders' Association, Beloit, Wis., Fred S. Idtse, Secretary.

Dutch Belted Cattle Association of America, Buchanan, Mich., R. E. Schwartz, Secretary.

Holstein-Friesian Association of America, Brattleboro, Vt., H. W. Norton, Jr., Secretary.

Draft Horses

American Clydesdale Association, 840 Exchange Avenue, Union Stock Yards, Chicago, Ill., Miss Margaret Coridan, Secretary.

American Shire Horse Association, 319 East 4th Street, Des Moines, Iowa, E. F. Fox, Secretary.

American Suffolk Horse Association, Bushnell, Ill., J. H. Truman, Secretary.

Belgian Draft Horse Corporation of America, Wabash, Ind., H. J. Brant, Secretary.

Percheron Horse Association of America, 9 Dexter Park Avenue, Union Stock Yards, Chicago, Ill., Ellis McFarland, Secretary.

Light Horses

American Hackney Horse Society, Merrick, Long Island, N.Y., Gurney C. Gue, Secretary.

American Saddle Horse Breeders' Association, Inc., 120 South 4th Street, Louisville, Ky., Charles J. Cronan, Jr., Secretary.

American Trotting Register Association, Inc., Goshen, N.Y., Charles E. Koons, Secretary.

Arabian Horse Club of America, Barrington, Ill., Alfred R. Watt, Secretary.

German, Hanoverian & Oldenburg Horse Association of America, Lafayette, Ind., G. R. Crouch, Secretary.

Tennessee Walking Horse Breeders Association of America, Lewisburg, Tenn., W. P. Murrey, Secretary.

The Jockey Club, 250 Park Avenue, New York, N.Y., Fred J. E. Klees, Registrar.

The Morgan Horse Club, Inc., 90 Broad Street, New York, N.Y., F. B. Hills, Secretary.

Ponies

American Shetland Pony Club, Bensonville, Ill., R. R. Tillman, Secretary.

The Welsh Pony & Cob Society of America, Lafayette, Ind., Miss Julia M. Wade, Secretary.

Jacks and Jennets

Standard Jack & Jennet Registry of America, 501 Scarritt Building, Kansas City, Mo., William E. Morton, Secretary.

Sheep

American Cheviot Sheep Society, Inc., Oneonta, N.Y., Mrs. Katherine S. Turrell, Secretary.

American Corriedale Association, 1007 Sheridan Street, Laramie, Wyo., Dr. F. S. Hultz, Secretary.

National Corriedale Sheep Association, 809 Exchange Avenue, Union Stock Yards, Chicago, Ill., Mrs. F. J. Moline, Secretary.

American Cotswold Registry Association, 807 Exchange Avenue, Union Stock Yards, Chicago, Ill., F. W. Harding, Secretary.

American & Delaine-Merino Record Association, Xenia, Ohio, Gowdy Williamson, Secretary.

Black Top & National Delaine Merino Sheep Breeders Association, Houston, Pa., I. Y. Hamilton, Secretary.

American Hampshire Sheep Association, 72 Woodland Avenue, Detroit, Mich., Mrs. Helen T. Belote, Secretary.

American Leicester Breeders Association, Cameron, Ill., A. J. Temple, Secretary.

American Oxford Down Record Association, Clayton, Ind., J. M. McHaffie, Secretary.

American Rambouillet Sheep Breeders' Association, Marysville, Ohio, Mrs. Dwight Lincoln, Secretary.

American Romney Breeders' Association, 200 Dairy Building, Oregon State College, Corvallis, Ore., H. A. Lindgren, Secretary.

American Shropshire Registry Association, Lafayette, Ind., Miss Julia M. Wade, Secretary.

American Southdown Breeders' Association, 203 Agricultural Building, State College, Pa., W. L. Henning, Secretary.

National Suffolk Sheep Association, 809 Exchange Avenue, Union Stock Yards, Chicago, Ill., Mrs. F. J. Moline, Secretary.

American Suffolk Sheep Society, Moscow, Idaho, C. W. Hickman, Secretary.

Continental Dorset Club, Hickory, Pa., J. R. Henderson, Secretary.

National Lincoln Sheep Breeders Association, Marlette, Mich., D. T. Knight, Secretary.

Karakul Fur Sheep Registry, Friendship, Wis., L. K. Brown, Secretary.

Goats

American Milk Goat Record Association, P.O. Box 196, Vincennes, Ind., Will L. Tewalt, Secretary.

American Angora Goat Breeders Association, Rocksprings, Tex., Mrs. Claudine Hampton, Secretary.

The American Goat Society, Inc., University Place, Lincoln, Neb., John P. Brox, Secretary.

Swine

American Berkshire Association, 410 S. 5th Street, Springfield, Ill., C. W. Mitchell, Secretary.

Cheshire Swine Breeders' Association, Sylvania, Pa., Fred W. Card, Secretary.

O. I. C. Swine Breeders Association, Goshen, Ind., O. C. Vernon, Secretary.

Chester White Swine Record Association, Rochester, Ind., L. P. Moore, Secretary.

Breeders' Chester White Record Association, 603 3rd Street, Des Moines, Iowa, C. C. Evans, Secretary.

United Duroc Record Association, Peoria, Ill., B. P. Evans, Secretary.

Hampshire Swine Registry, Commercial National Bank Building, Peoria, Ill., E. M. Harsch, Secretary.

National Mule Foot Hog Association, De Graff, Ohio, O. C. Kreglow, Secretary.

American Poland China Record Association, 1 Dexter Park Avenue, Union Stock Yards, Chicago, Ill., George W. Davies, Secretary.

National Poland China Record, Winchester, Ind., C. G. McCahan, Secretary.

Standard Poland China Record Association, Maryville, Missouri, J. E. Rush, Sec.

National Spotted Poland China Record Association, Bainbridge, Ind., F. L. Obenchain, Secretary.

American Spotted Poland China Association, Moberly, Mo., Van G. Sutliff, Secretary.

Yorkshire Swine Breeders Association, 1001 La Fond Street, St. Paul, Minn., Harry Krum, Secretary.

National Hereford Hog Record Association, New Sharon, Iowa, A. W. Way, Secretary.

American Tamworth Swine Record Association, Ames, Iowa, W. T. Barr, Secretary.

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